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LIFE ON THE EFFECTIVE BUBBLE: EXOCRINE SECRETION DELIVERY SYSTEMS (ESDS) AND THE EVOLUTION AND CLASSIFICATION OF BEETLES IN THE FAMILY HYDRAENIDAE (INSECTA: COLEOPTERA)

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Abstract

Exocrine secretion delivery systems (ESDS) of aquatic beetles in the family Hydraenidae are described for the first time, and used to clarify phylogenetic relationships within the family. ESDS components include secretion-grooming behavior, surface cuticular specializations for secretion delivery, locations of exocrine pores, and locations and densities of ductules and end-apparatus of exocrine glands. ESDS structures are illustrated with scanning electron micrographs and drawings. The systems function, at least in part, to maintain the respiratory bubble by making the cuticular surfaces within the bubble, and especially at critical marginal areas of the bubble, clean of hydrophilic microbes and debris. Secretion-grooming is performed out of the water, often with the beetle "on edge," the legs on the "free" side acting together in patterns of secretion spreading and mutual rubbing. Spreading of secretions on the cuticular surface, movement of secretions between body areas, and cleaning of the cuticle by scraping and rubbing are achieved by specialized patches and rows of setae on the legs.

A reclassification of the family is proposed, based in large part on putative synapomorphic characters and morphoclines of the ESDS and antennal pocket. The following suprageneric taxa are proposed and characterized: Orchymontinae, new subfamily; new tribes Madagastrini, Parhydraenini, and Ochtheosini; and new subtribes Meropathina, Neochthebiina, Protochthebiina, and Enicocerina. In the Ochthebiinae, the "subgenera" *Calobius* Wollaston, *Cobalius* Rey, *Liochthebius* J. Sahlberg, and *Notochthebius* Orchymont are reduced to synonymy with *Ochthebius*, whereas full generic status is proposed for *Aulacochthebius* Kuwert and *Enicocerus* Stephens. In the Hydraeninae, *Hydraenopsis* Janssens and *Spanglerina* Perkins are synonymized with *Hydraena* Kugelann, whereas *Haenydra* Rey and *Hadrenya* Rey are considered valid subgenera.

The following new genera and new species are described: *Haptaenida huggerti* (Ecuador), *Madagaster steineri* (Madagascar), *Ochtheosus fungicolus* (Chile), *Protochthebius satôi* (Nepal), *Protozantaena labrata* (South Africa), *Pneuminion velamen* (South Africa), and *Tympallopatrum longitudum* (Australia). *Davidraena bacata* n. sp. is described from India. Keys to the subfamilies, tribes, and genera of Hydraeninae, and tribes, subtribes, and genera of Ochthebiinae are given.

Introduction

Microhabitats, Behavior, and Morphology

Members of the family Hydraenidae are tiny beetles, the majority of which are adapted for marginal life in the microscopic aquatic world. These aquatic beetles breathe by means of an air reservoir covering the ventral surface. Hydraenids cannot swim, but are able, due to their small size and ventral bubble, to "walk," upside down, on the water's surface film. The respiratory bubble is pivotal to the ability of these beetles to effectively utilize the microaquatic world. This paper describes the varied and intricate ways that the hydraenid bubble is formed and

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maintained, and uses these new character systems to clarify relationships and classification of the family.

Hydraenid beetles live in a wide variety of aquatic habitats. Although most species live at the sandy-gravelly margins of streams and ponds (Perkins, 1981), some species live in stagnant water (Cuppen, 1993), a very small percentage of the species are semiaquatic or humicolous (Perkins and Balfour-Browne, 1994), and one species, described herein, is fungicolous.

Three hydraenid genera, *Ochthebius, Hydraena,* and *Limnebius,* have specialized "exocrine secretion delivery systems" (ESDS), described below, that help maintain the respiratory bubble. Members of these three genera, while out of the water, perform a series of secretion-grooming motions with the legs. The leg actions, principally repetitive movements of the femora and tibiae, correlate with the locations of exocrine gland pores and associated cuticular elements such as specialized setae, cuticular ridges, and secretion grooves.

In *Hydraena* and *Limnebius* the full repertoire of secretion-grooming is performed with the beetle "on edge" (Fig. 9A, 25A), with the legs on one side "in the air," acting in complicated concert to perform the spreading, transferral, and cleaning actions. This behavior not only spreads the secretions, it also coordinates the evolution of ESDS components located on different body regions.

The genera *Ochthebius, Hydraena,* and *Limnebius,* are conspicuously "successful"; that is, they are by far the most speciose in the family and are cosmopolitan, or nearly so, in distribution (Fig. 71). The ability to make the cuticle resistant to wetting within, and especially at critical marginal areas of the respiratory bubble, is obviously a necessary prerequisite for effective utilization of aquatic habitats by hydraenids. It seems likely, therefore, that the possession of a specialized ESDS is a major reason why these three genera have attained relative success in the family. Plesiomorphic (and less successful) genera lack specialized ESDS.

ESDS components (i.e., locations, structures, and behavior) of *Ochthebius, Hydraena,* and *Limnebius* differ markedly one from the other. This evidence strongly suggests that ESDS specializations for aquatic existence evolved independently in these three genera, each from a different, less specialized ancestor. Whether these ancestors were aquatic, semiaquatic, or perhaps even humicolous, is an open question. The habits of the common ancestor of the family are an even more remote question, but the likelihood of humicolous habits seems to be increased by these findings.

In addition to the bubble maintenance components, ESDS also include exocrine glands that secrete onto the wet portions of the cuticle (i.e., outside the bubble). The locations, end-apparatus, and pore distributions of some of these glands are described, and some probable functions of the secretions are discussed below. Variations in ESDS within taxa are shown to be very effective in clarifying some long-standing systematic problems, especially in the Ochthebiinae.

In most insects the antennae serve only olfactory and sometimes tactile functions. In hydraenids the antennae also serve as part of the respiratory system: they are used to break the water's surface film so that the air reservoir ("bubble") can be replenished. The last five articles of the antenna form a "club" that, in addition to having olfactory sensilla, is clothed in hydrofuge hairs and therefore water repellent (Fig. 1A).

When not performing its essential and often repeated act of being raised to break the surface film, the antenna is held beneath the eye, with the club protected by being placed behind the eye and/or in the "antennal pocket" of the adjacent prothorax (Fig. 2, 19A). Exocrine glands and cuticular areas behind the eye and on the prothorax have evolved together, resulting in an integrated system that (1) protects the antennal club, (2) helps maintain the respiratory bubble, and (3) provides sensory receptors for molecules brought into the postocular area by the antennal club.

The complexities of the antennal pocket vary among the taxa, providing many previously undescribed characters that are essential to a better understanding of the evolution and classification of the family.

Functions of Exocrine Secretions

Studies of aquatic beetles in other families, such as the diving beetles (Dytiscidae) and related adephagan families, have shown that some exocrine gland secretions are hydrophilic and serve as wetting agents in addition to being antimicrobial (Dettner, 1985). The beetle's cuticle, when not coated with a secretion, is hydrophobic; this water-repellant condition can prevent tiny beetles from breaking through the surface film to enter the water (Dettner and Schwinger, 1980). This hydrophobic state is changed to a hydrophilic one by the beetles (while out of the water) using the legs to spread hydrophilic exocrine secretions over the body surface. The air reservoir in these adephagan beetles is under the elytra, and the entire body surface (except the abdominal apex) is wet when the adult is in the water.

In contrast to adephagan aquatic beetles, many aquatic bugs have ventral hydrofuge hairs that hold an air reservoir. Recently Kovac and Maschwitz (1989, 1991) gave experimental evidence that the exocrine secretion produced by the metathoracic gland of aquatic bugs (Pleidae, Corixidae, Naucoridae) functions to kill bacteria. The hydrofuge hairs become wettable if covered with hydrophilic bacteria, the respiratory bubble is consequently lost, and the animals drown. The secretion, consisting principally of hydrogen peroxide, is rubbed on the hydrofuge pubescence by the legs. Kovac and Maschwitz (1989, 1991) termed this behavior "secretion-grooming."

Hydraenid beetles differ markedly from aquatic adephagan beetles (i.e., dytiscids) and aquatic bugs in both basic structural morphology and behavior. Dytiscids and aquatic bugs are very active swimmers, whereas hydraenids cannot swim, but instead crawl over the substrate. Hydraenids have a ventral air bubble, but replenish it by using the antennae to form an air funnel to the surface, instead of using the tip of the abdomen. The secretion-grooming behavior of hydraenids is very different from that of aquatic bugs, and the secretions lack any indication of "foaming" like that produced by hydrogen peroxide secretions.

Although tests of the physicochemical properties of the secretions produced by hydraenids have not been made, it seems reasonable to assume a hydrophilic nature for chemicals that are secreted onto surfaces that are wet when the beetle is in the water (i.e., surfaces outside the bubble). Since insect cuticle is hydrophobic, wettability via secretions is essential to prevent these tiny beetles from becoming "trapped" in the water's surface film. In contrast, secretions produced onto surfaces within and at the margins of the respiratory bubble certainly cannot be hydrophilic, but must be hydrophobic.

Antimicrobial (i.e., defensive) properties are also expected for hydraenid exocrine secretions, as was demonstrated for dytiscids, etc., by Dettner and Schwinger

(1980). The hydrogen peroxide secretion of aquatic bugs is effective against bacteria but ineffective against protozoa (sessile ciliates) that colonize only the wet parts of the cuticle (Kovac and Maschwitz, 1989). The sessile ciliates' nonsusceptibility to the antiseptic secretion does not impair the bugs' respiration, because the ciliates attach outside the respiratory bubble. However, protozoa attaching to or at the bases of setae that function to maintain a special part of the bubble, such as adjacent to the antenna in hydraenids, could have negative effects on respiration and on chemoreceptive functions integrated with the air capture system.

Over the past 20 years there has been a steady increase in knowledge of defensive exocrine secretions of Coleoptera (Dettner, 1987). However, these studies have involved a relatively small part of the order. About 175 families of Coleoptera are currently recognized (Crowson, 1981; Lawrence and Newton, 1995). Of these, only about 32 families have had some representatives studied for the comparative distribution of exocrine glands and the chemistry of their secretions (Dettner, 1987). Of these 32 families, only about ten have had the adult stage of some species studied by three methods, that is, SEM (for associated surface structures), histological/cytological preparations, and chemical analysis of secretions.

Several of the genera that have been studied are members of huge families (e.g., Staphylinidae, Tenebrionidae, Scarabaeidae, Chrysomelidae), and can scarcely represent the immense bio- and morphodiversity of these families. The matter of function is further clouded since glands with similar cytology have been found to secrete very different chemicals. Functions of exocrine secretions can be as diverse as sex pheromones in successive behavior patterns, defensive repellants, organic carriers, surfactants, penetrators, evaporation retardants, water repellants, and antimicrobials.

Even cockroaches, with perhaps the best studied glandular exocrine systems, are replete with unknowns. For example, Brossut (1983) identified 43 exocrine products from only ten cockroach species, and emphasized that functions could not be assigned to most of those chemicals in the absence of behavioral studies.

Of the Coleoptera exocrine systems described in the literature, I was unable to find any that are similar to those of hydraenids. Taxa included in this review are: Anisotomidae (Cazals and Juberthie-Jupeau, 1983); Anobiidae (Levinson et al., 1983); Bruchidae (Biemont et al., 1990); Carabidae (Forsyth, 1970; Juberthie and Piquemal, 1977); Catopidae (Martin, 1977); Chrysomelidae (Kendall, 1972); Dermestidae (Hammack et al., 1973); Dytiscidae (Forsyth, 1968; Dettner and Schwinger, 1980; Dettner, 1985); Gyrinidae, Haliplidae, and Noteridae (Forsyth, 1968); Pselaphidae (Cammaerts, 1974; Hill et al., 1976); Pyrochroidae (Dettner, 1984); Scarabaeidae (Pluot-Sigwalt, 1986, 1991); Scolytidae (Happ et al., 1971); Staphylinidae (Pasteels, 1968*a*, 1968*b*, 1969; Araújo, 1978; Peschke, 1978, 1986; Klinger, 1980; Araújo and Pasteels, 1987; Peschke and Metzler, 1987; Dettner and Reissenweber, 1991; Johannes et al., 1993); Tenebrionidae (Roth, 1943; Wigglesworth, 1948; Roth and Eisner, 1962; Eisner et al., 1964; Delachambre, 1973; Tschinkel, 1975*a*, 1975*b*; Tschinkel and Doyen, 1980).

Purpose and Organization

The purposes of this paper are to describe in detail previously unknown character systems, including behavioral components, of the specialized ESDS of the genera *Ochthebius, Hydraena,* and *Limnebius*; describe and compare cuticular parts of corresponding body regions in all genera of the family; and apply the results of the comparative morphological study to the classification of the family.

The general organization of the paper is as follows: (1) the secretion-grooming behavior and functional anatomy of the ESDS of *Ochthebius, Hydraena,* and *Limnebius* are described; (2) a revised classification of the family is presented, including descriptions and discussions of the ESDS and corresponding cuticular parts and body regions in all genera and subgenera, discussion of plesiomorphic and putative synapomorphic character states, and formal descriptions of new taxa; (3) taxonomic keys utilizing the new character systems are provided; and (4) concluding remarks are given.

A list of the taxa that were studied in transparency mounts, and designations of new combinations, is given in Appendix 1. An index to the major topics is given in Appendix 2.

MATERIALS AND METHODS

Microtechniques

Specimens were prepared for transparency mounts by the following steps: (1) dry specimen placed in 10% potassium hydroxide at room temperature; (2) after appropriate maceration with potassium hydroxide (usually overnight), specimen transferred to a 3% solution of hydrogen peroxide; (3) after appropriate decolorization in hydrogen peroxide (usually minutes), specimen transferred to distilled water; (4) after at least 30 minutes in distilled water, specimen transferred to 80% ethanol for a few minutes, and then into 95% ethanol; and (5) after air bubbles have disappeared, specimen transferred to 80% ethanol for a few minutes (or temporarily stored in 80% ethanol).

Cleared and decolored specimens were studied with a compound microscope, either as depression slide preparations in lactic acid (and later stored in glycerin on microslides), or slide mounted in balsam, using standard techniques. Some specimens were stained with acid fuchsin before being studied in transparency mounts.

Specimens used for scanning electron microscopy were cleaned in a sonic cleaner (in 80% ethanol), then dehydrated in 95% ethanol before being placed in acetone (for a few minutes). In a few instances, specimens that had been studied as transparency preparations were subsequently removed from microslides, cleaned, and studied by SEM, thereby allowing a one-to-one correlation between internal and surface structures.

Illustrations of male genitalia and other body parts were prepared with the aid of a drawing tube attached to a compound microscope, using temporary transparency mounts in lactic acid. For storage, the aedeagus and dissected body parts of each specimen are in glycerin in a glass microvial which is affixed to the pin of the specimen.

Acronyms of Structures

The following acronyms are used for external cuticular features: **ah-border**, anterior hyaline border of the pronotum; **gap-setae**, genal antennal pocket setae; **hap-setae**, hypomeral antennal pocket setae; **hh-border**, hypomeral hyaline border; **hp-sensilla**, hypomeral paired sensilla; **hsd-carina**, hypomeral secretion delivery carina; **hsd-sulcus**, hypomeral secretion delivery sulcus; **hsd-surface**, hypomeral secretion delivery surface; **lh-border**, lateral hyaline border of the prothorax; **pa-groove**, postocular antennal groove of the head; **psd-setae**, postocular secretion delivery setae of the head; **psd-sulcus**, postocular secretion delivery sulcus of the head; **sa-groove**, subocular antennal groove of the head.

SECRETION-GROOMING BEHAVIOR AND FUNCTIONAL ANATOMY

Genus Ochthebius

Secretion-grooming Behavior.—The secretion-grooming behavior of *Ochthebius* described below is based on observations of two distantly related species from North America, *O.* (sensu stricto) *interruptus* and *O.* (*Asiobates*) *puncticollis.* Aspects of the biology and taxonomy of these species are given by Perkins (1976, 1981).

Given the behavioral similarities observed in these two species, and given the phylogenetic distance separating them, it is perhaps reasonable to expect similar behavior in most species of the genus that have similar specialized exocrine structures and similar leg morphology. Of course observations of many other species are necessary to confirm this prediction.

The individuals of *Ochthebius* observed thus far did not position themselves "on edge," as is described below for *Hydraena* and *Limnebius.* Rather, the body is raised and balanced on some of the legs, while the "free" legs perform the secretion-grooming.

One of the first actions in secretion-grooming is the extension and deflexion of the prothorax. This action opens the hydrofuge area surrounding the mesothoracic spiracles, allowing the removal of water and any other contaminants. As described below, much of the leg actions take place in the hydrofuge area at the juncture of the prothorax and the mesosternum. The intersegmental membrane separating these two areas contains the large mesothoracic spiracles.

Often the prothorax is twisted from side to side, and sometimes "pulsates" in a deflexing motion. Sometimes the head is pressed upward against the anterior hyaline border (while the pronotum is deflexed). These actions probably move water to areas where it can be removed and/or will evaporate more rapidly.

Two kinds of movements of the front leg result in rubbing against the posteroventral angle of the eye. In this location are specialized (shaped like eyelashes) postocular secretion delivery setae (henceforth termed psd-setae) that are adjacent to a secretion reservoir, the postocular secretion delivery sulcus (= psd-sulcus; e.g., Fig. 1). These rubbing actions may occur while the beetle is balanced on a total of three (the "tripod"), four, or five legs.

Usually the initial secretion-grooming leg behavior ("step 1") is a repeated probing at the area of the psd-setae with the spines at the apex of the protibia. This action surely causes a spreading of the exocrine secretion onto the protibial apex; it probably additionally forces more secretion out of the psd-sulcus by pressing against and deforming the thin cuticular rim. Sometimes, after the probing, the protibia is rubbed against the prosternum.

The second kind of leg behavior resulting in rubbing the psd-setae ("step 2") occurs when the protibia strokes across the top of the eye: at the end of this motion the distal area of the profemur comes into contact with the psd-setae. The area of the profemur that rubs the psd-setae is armed with stout setae, forming the "distal spine cluster" (Fig. 5).

Immediately after rubbing the psd-setae, the profemur is brought backward and the distal spinose area is rubbed ("step 3") against the ventral surface of the posterolateral area of the prothorax, where the lateral and the hypomeral hyaline borders are contiguous (e.g., Fig. 31).

The repeated action of rubbing the profemoral distal spine cluster against the psd-setae (step 1), and then *immediately* rubbing the hyaline borders at the hind

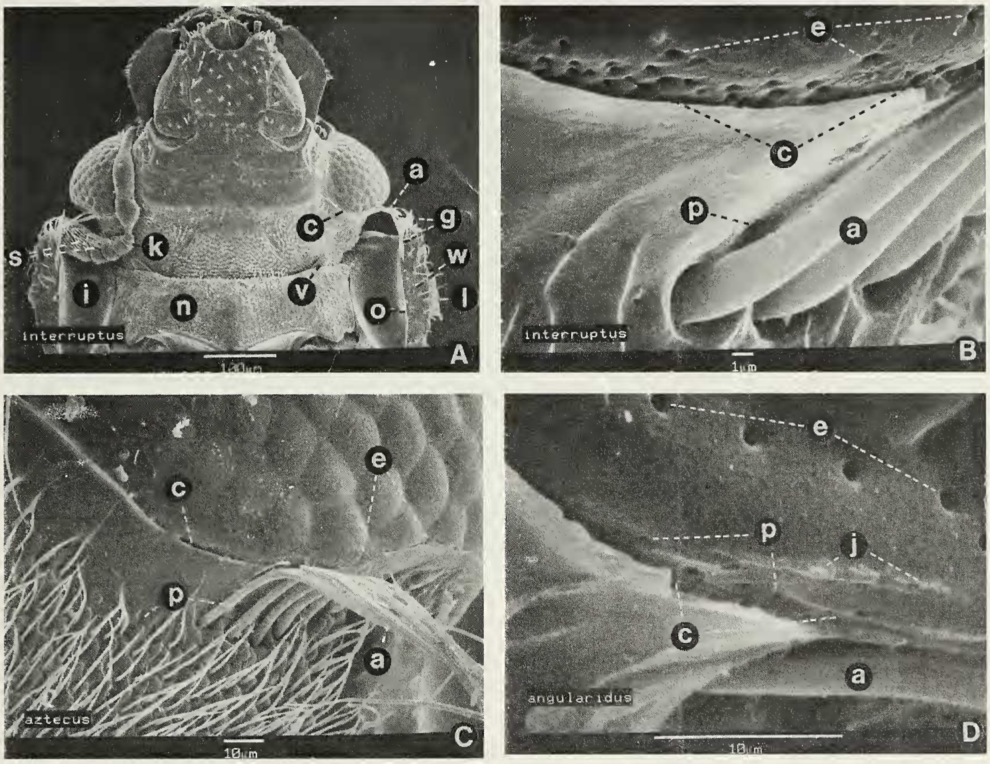


Fig. 1.—*Ochthebius*, venter of head and prothorax, and details of psd-sulcus area. A, B. *O. interruptus*. C. *O. aztecus*. D. *O. angularidus*. Structures: (a) psd-setae, (c) psd-sulcus (rim broken off in D), (e) periocular exocrine pores, (g) hap-setae, (i) hypomeral antennal pocket, (j) cuticular ridge, (k) cupule article of antenna, (l) lh-border, (n) prosternum, (o) hh-border, (p) exocrine pores in psd-sulcus, (s) sensilla of antennal club, (v) cervical sclerite, (w) wet-hypomeron.

angles of the prothorax (step 2), surely results in the transferral and spreading of the exocrine secretions present on the psd-setae and in the psd-sulcus. Cleaning surfaces of debris and microbes certainly also occurs during these movements, by scraping with the stiff spines on the profemur.

Another distinct rubbing behavior (the "backstroke") involves the middle legs, and occurs while the beetle is balanced on one (see below) or both of the front legs, and both of the hind legs. The middle legs, usually in unison, are brought forward until the femur of each is held tightly against the cuticle beneath the posterolateral angle of the pronotum (i.e., against the lateral hyaline border and posterior extreme of hypomeral hyaline border); the mesotibiae also are held tightly against the cuticle. The middle legs then extend posteriorly, again usually in unison. During this stroke the mesofemur rubs against the lateral part of the mesosternum, and the mesotibia rubs against the metasternum and/or the elytral epipleuron, especially the hydrofuge pubescent anterior part of the epipleuron.

Sometimes the actions of the middle legs and one front leg are integrated. During this behavior (the "tripod") the beetle balances on three legs, one front and the two hind legs. While in this balanced position, the middle legs perform the "backstroke." Concurrently, the "free" front leg performs the step 2 and then step 3 behaviors (sometimes, but not always, preceded by step 1).

After step 3, the front leg then engages in rapid mutual rubbing with the adjacent middle leg ("step 4"). Most of this mutual rubbing involves the femora, but the tibiae are also rubbed together. Initially the opposing faces of the two legs are rubbed together, but the legs are often "crossed over" and rubbed on the other faces. Sometimes the mesotibia is placed on top of the profemur, and rubs back and forth against the distal spine cluster. The opposing faces of the femora (posterior of profemora and anterior of mesofemora) each have a cluster of spinose setae (Fig. 5, 6) that are involved in this mutual rubbing.

Sometimes during step 4 (mutual rubbing) the pro- and mesofemora are alternately pressed tightly against and rubbed back and forth in the hypomeral/lateral hyaline border area. Like the profemur, the mesofemur has a distal spine cluster (Fig. 6) that contacts the hypomeral area during this behavior. During the "tripod," the step 2-3-4 behavioral sequence of the front leg is repeated several times while the middle legs are repeating the "backstroke" pattern.

The hind legs do some rubbing of the elytral epipleura, and often do mutual metatibial rubbing; the latter behavior is performed while the beetle is balanced on the front and middle legs. While stroking the elytral epipleuron, the metatibial spines probably also stroke the abdominal hydrofuge pubescence bordering the epipleuron. No extensive rubbing of the upper surface of the elytron was observed.

Following is a summary of the secretion-grooming leg movements: step 1: protibial apex probes at the psd-setae on the postocular area; step 2: protibia strokes across the dorsal surface of the eye, and at the end of this motion the distal spine cluster of the profemur rubs the psd-setae; step 3: distal spine cluster of the profemur rubs back and forth against the ventral surface of the hypomeral and lateral hyaline borders at the posterolateral area of the prothorax; step 4: profemur and protibia rub against the mesofemur and mesotibia of the adjacent middle leg; backstroke: middle legs, usually in unison, stroke backward; tripod: beetle balanced on one front leg and the two hind legs while "free" front leg and middle legs perform secretion-grooming behavior.

ESDS Cuticular Components.—In *Ochthebius* the postocular area and the hypomeral antennal pocket form a complex region of integrated structures (Fig. 1, 2). These structures include exocrine pores, secretion collecting reservoirs, secretion delivery setae, various forms of cuticular hydrofuge, thin hyaline margins, and the antenna.

The locations of these structures, and observations on living beetles (described above), strongly suggest that these structures function, at least in part, to help maintain the respiratory bubble around the antennal club. This is a critical marginal part of the bubble, an area that is subject to loss of hydrofuge properties resulting from the repeated movement of the antenna in and out of the bubble during air capture.

Antennal Pocket and Hyaline Borders.—A characteristic feature of the genus *Ochthebius* is the presence of thin, flexible, transparent hyaline borders on the prothorax (Fig. 28, 31). All species of the genus (as herein defined) have four hyaline borders: anterior (ah-border), posterior (ph-border), lateral (lh-border), and hypomeral (hh-border). Very rarely, the lh-border may be rudimentary or perhaps secondarily lost. Equally rarely, the entire pronotum may be margined with a hyaline border, the lh-border being continuous with the ah- and ph-borders.

The antennal pocket of the prothorax, in which the antennal club is held, is bordered by two hyaline margins, the ah-border that forms the anterior margin of

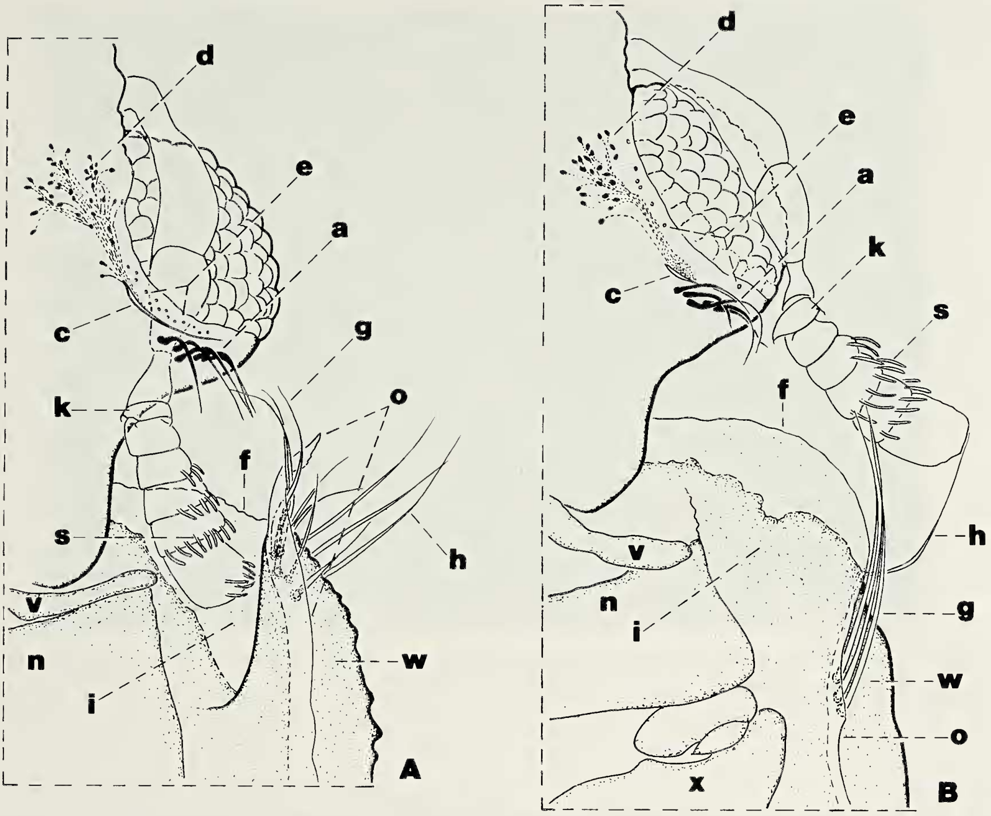


Fig. 2.—*Ochthebius*, ventral aspect of left side of head and adjacent area of prothorax, showing external cuticular features and internal end-apparatus and ductules (d) of exocrine glands. A. *O. glaber*. B. *O. quadricollis*. Structures: (a) psd-setae, (c) psd-sulcus, (d) end-apparatus and ductules of exocrine glands, (e) periocular exocrine pores, (f) ah-border, (g) hap-setae, (h) anterolateral pronotal setae, (i) hypomeral antennal pocket, (k) cupule article of antenna, (n) prosternum, (o) hh-border, (s) sensilla of antennal club, (v) cervical sclerite, (w) wet-hypomeron, (x) procoxa.

the antennal pocket, and the hh-border that forms the lateral margin of the antennal pocket (Fig. 2:f, o). In many species these two hyaline margins are contiguous at the anterolateral angle of the prothorax (e.g., Fig. 28C).

The ventrally located hh-border (o in Fig. 1, 2, 28) forms the lateral limit of the prothoracic part of the respiratory bubble. The hh-border gradually reduces in height toward the posterior part of the hypomeron, and in its posterior part becomes contiguous with (but perpendicular to) the lh-border. Often the hh-border is indicated dorsally on the lh-border by a corresponding, shallowly impressed line.

The hh-border separates each hypomeron into two areas (Fig. 1, 2, 28): the lateral area (outside the bubble) that can be termed the wet-hypomeron (w), and the medial area that consists of the antennal pocket (i) and the postcoxal projection (Fig. 28:d) of the pronotum (the antennal pocket and the postcoxal projection can be jointly termed the bubble-hypomeron).

The lh-border is located posterolaterally (at least), its posterior extreme being contiguous with the ph-border. The degree of development and the shape of the

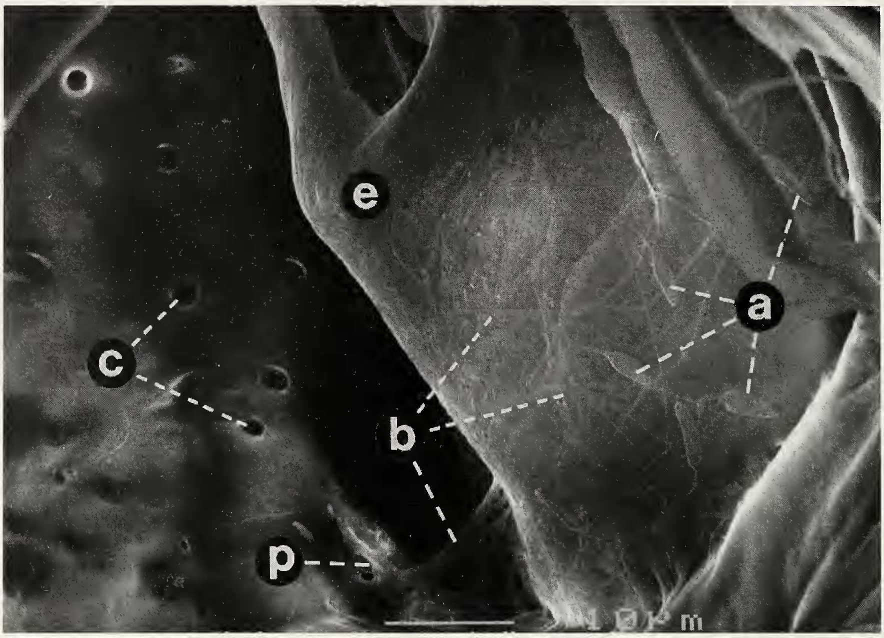


Fig. 3.—*Ochthebius gruwelli,* internal view of head (macerated with sodium hydroxide). Structures: (a) end-apparatus of exocrine glands, (b) ductules, (c) sockets of psd-setae, (e) cuticle of internal wall of eye, (p) internal surface of psd-sulcus.

lh-border varies among the species; usually the border occupies about the posterior one-half. The ah-border and the ph-border form the anterior and posterior margins of the prothorax respectively and (when the prothorax is moved such that gaps exist between the ah-border and the head, or the ph-border and the elytra) form the anterior and posterior margins of the bubble.

Peri- and Postocular Exocrine Pores.—Exocrine pores near the margin of the eye are of two types based on differences in size, positions, and internal cuticular components. These two types can be termed periocular pores and postocular pores.

Periocular pores are about 1.0 µ in diameter (about twice as large as postocular pores) and are located around the periphery of the eye (e.g., Fig. 1:e). Transparency whole-mount preparations do not show end-apparatus and ductules leading to these pores, suggesting that the associated glands are probably Type I (Noirot and Quennedey, 1974, 1991). Periocular pores are present in all hydraenids that have been studied, and are therefore probably an ancestral condition.

Postocular pores are smaller, about 0.5 µ in diameter, and are clustered near the posteroventral angle of the eye (e.g., Fig. 1B, D). Internally each of these pores is connected to a long ductule which terminates in a sperm-shaped end-apparatus (Fig. 2A:d, B:d; 3:a). The exocrine glands supplying these pores are therefore Type III (Noirot and Quennedey, 1974, 1991).

In many species groups the periocular pores are situated on a shelf-like area, and are distinctly separated from the postocular pores (e.g., Fig. 1D; 29B, D). In some species groups the shelf-like area is lacking and the two types of pores are adjacent to one another (e.g., Fig. 1B, C). This latter condition may be correlated with overall eye shape (i.e., species with more convex eyes lack the shelf-like area).

Postocular Secretion Delivery Sulcus.—In members of *Ochthebius* the postocular pores are located in a secretion reservoir, the postocular secretion delivery (psd-) sulcus (e.g., Fig. 1B, D). The psd-sulcus is formed between the angulate margin of the eye and a thin cuticular ridge. If this ridge is broken, the postocular pores are revealed within the psd-sulcus (e.g., Fig. 1D).

Postocular Secretion Delivery Setae.—Immediately posterior to the psd-sulcus is a group of specialized setae, the postocular secretion delivery (psd-) setae (e.g., a in Fig. 1C, 2A). The psd-setae are bent adjacent to the psd-sulcus such that the secretion in the psd-sulcus spreads along the setae (spreading aided by antennal movements and grooming behavior with the front legs). In some SEM preparations (uncleaned specimens) the psd-setae are coated with the secretion (e.g., Fig. 1C). The psd-setae take various forms that are indicative of generic limits (see below).

Hypomeral Antennal Pocket Setae.—In *Ochthebius* the tips of the psd-setae are in contact with the tips of setae arising on the prothorax, the hypomeral antennal pocket (hap-) setae (e.g., g in Fig. 2A, B; 28C). Secretions on the psd-setae would presumably be spread onto these prothoracic setae by the antenna as it moves in and out of the antennal pocket, and/or by leg movements during grooming behavior.

Hypomeral Exocrine Glands.—Solitary (nonclustered) exocrine pores are found in the antennal pocket and on the wet-hypomeron. In the nonhydrofuge pubescent part of the antennal pocket the pores vary in density, but usually are quite sparse, although often slightly denser adjacent to the hypomeral hyaline border (Fig. 4B, C). In most species of *Ochthebius* (sensu stricto), pores are also sparse on the wet-hypomeron (for example, in *O. marinus* there are about 8–12 pores on the wet-hypomeron) and solitary, and lack large or obvious (in whole mounts) end-apparatus. In contrast, the wet-hypomeron of some species of *Enicocerus, Gymnochthebius,* and *Ochthebius* (*Asiobates*) have clusters of exocrine pores that are supplied with well-developed end-apparatus (Fig. 35C, D; 36C, D; 51A, B, C;—see discussion under *Enicocerus*).

Femoral Setae.—The femoral setae of two species, *O.* (sensu stricto) *interruptus* and *O.* (*Asiobates*) *puncticollis* are illustrated (Fig. 5–8). These two species differ in microhabitat, *O. interruptus* being found at or close to the waterline, whereas *O. puncticollis* is often found farther away from the waterline, on sandy-gravelly stream banks (Perkins, 1976).

These ecological differences correspond with differences in the femoral setal morphology. In *O. interruptus,* the "more aquatic" species, the femora have numerous elongate and flexible setae, placed near the margins of the pro- and mesofemora (Fig. 5A, 6A), and generally distributed over the anterior (substrate) face of the metafemur. In marked contrast, the meso- and metafemora of the less aquatic *O. puncticollis* lack these elongate, slender setae, instead having the anterior (substrate) surfaces with numerous, short, and stout setae (Fig. 6B, 8). In addition, the pro- and mesofemora of *O. puncticollis* have more setae in the distal spine cluster.

It seems reasonable to postulate that the elongate setae of *O. interruptus* function in more of a sensory capacity, to detect water movement, whereas the stout setae of *O. puncticollis* increase crawling efficiency. Careful study of the femoral

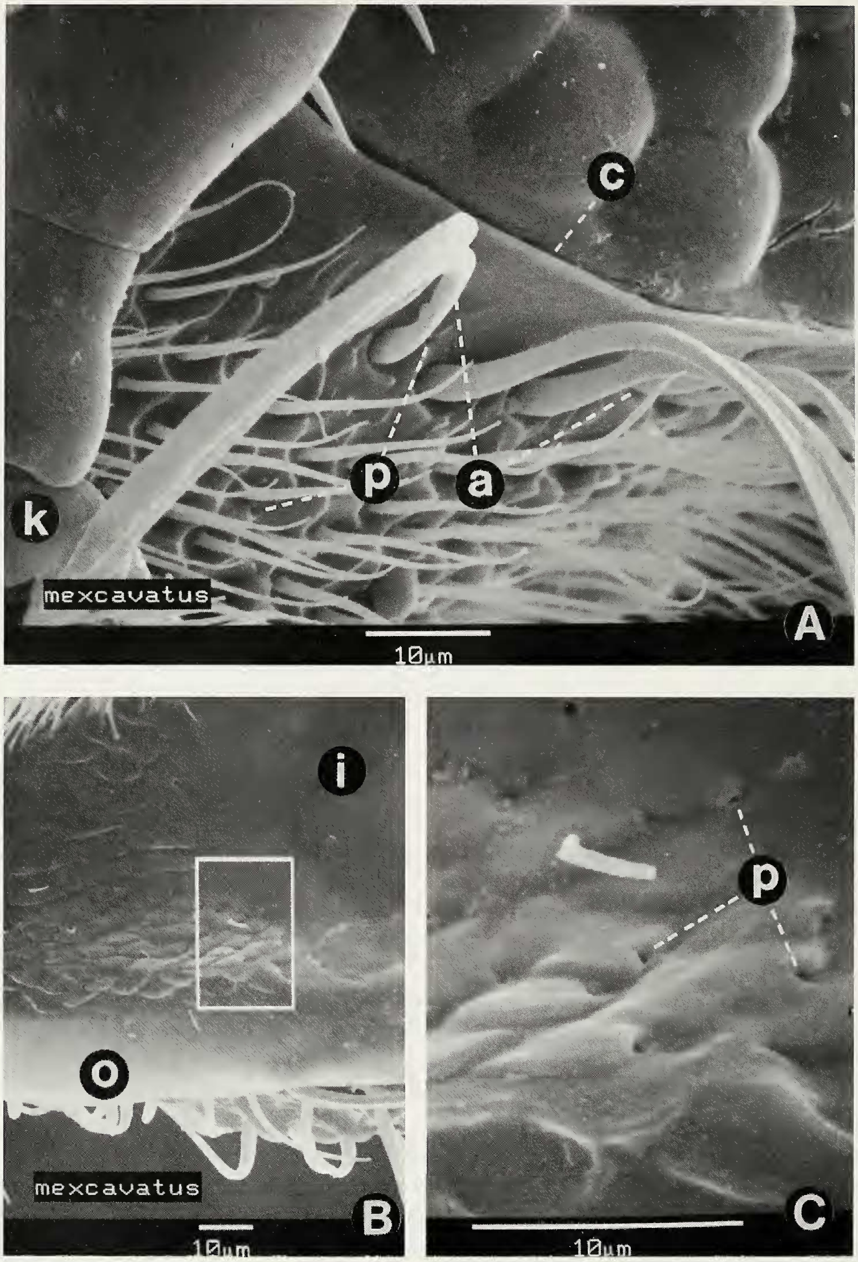


Fig. 4.—*Ochthebius mexcavatus.* A. Psd-sulcus and adjacent area. B. Prothoracic hypomeron, left side. C. Rectangular area in B, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (i) hypomeral antennal pocket, (k) cupule article of antenna, (o) hh-border, (p) exocrine pores.

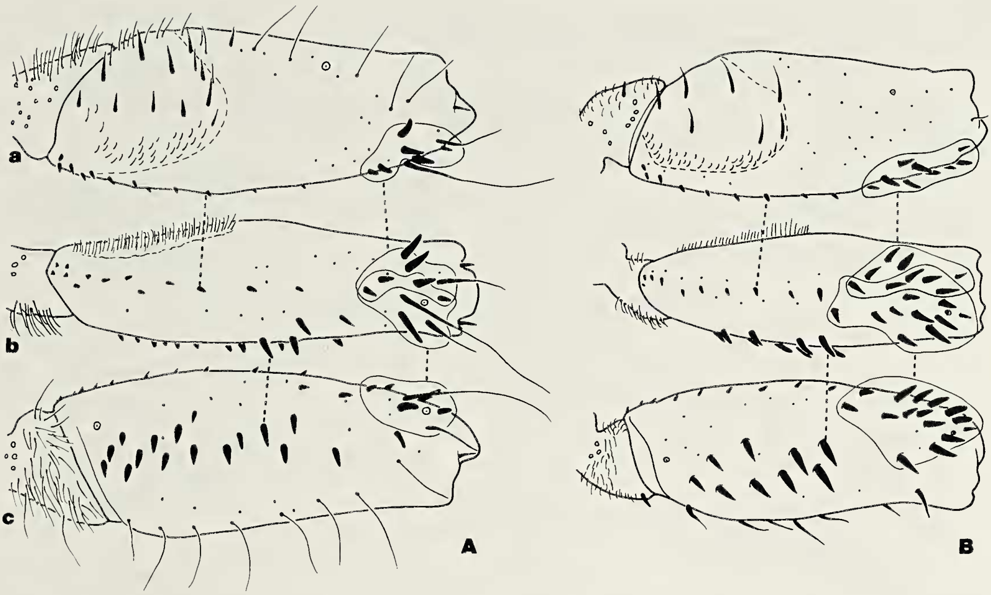


Fig. 5.—Profemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae of distal spine cluster indicated by dashes and loops. A. *Ochthebius interruptus*. B. *O. puncticollis*.

setae of ochthebiines should prove useful for predicting microhabitat preferences of species.

Function of the Hyaline Borders.—The lateral hyaline borders of *Ochthebius* take many shapes and have been important historically in the taxonomy of the genus. However, the hypomeral hyaline border has been overlooked by previous

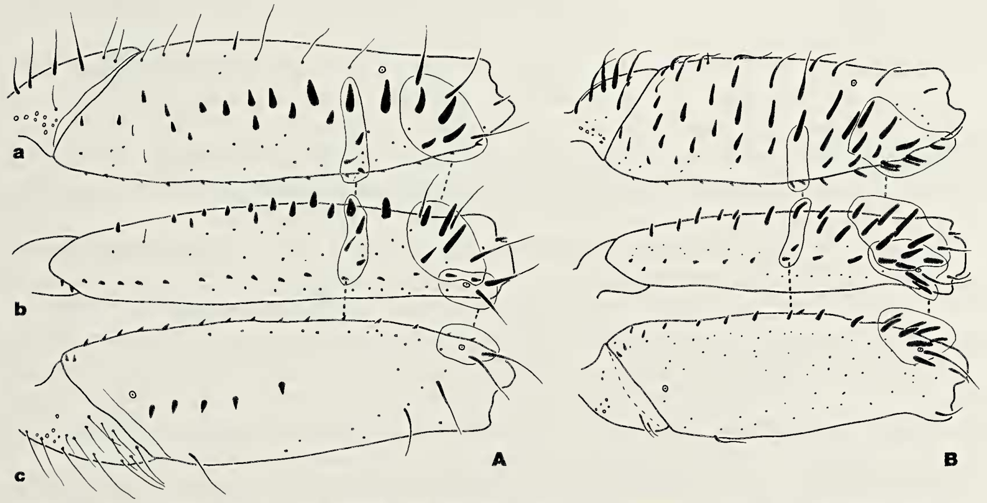


Fig. 6.—Mesofemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae of distal spine cluster indicated by dashes and loops. A. *Ochthebius interruptus*. B. *O. puncticollis*.

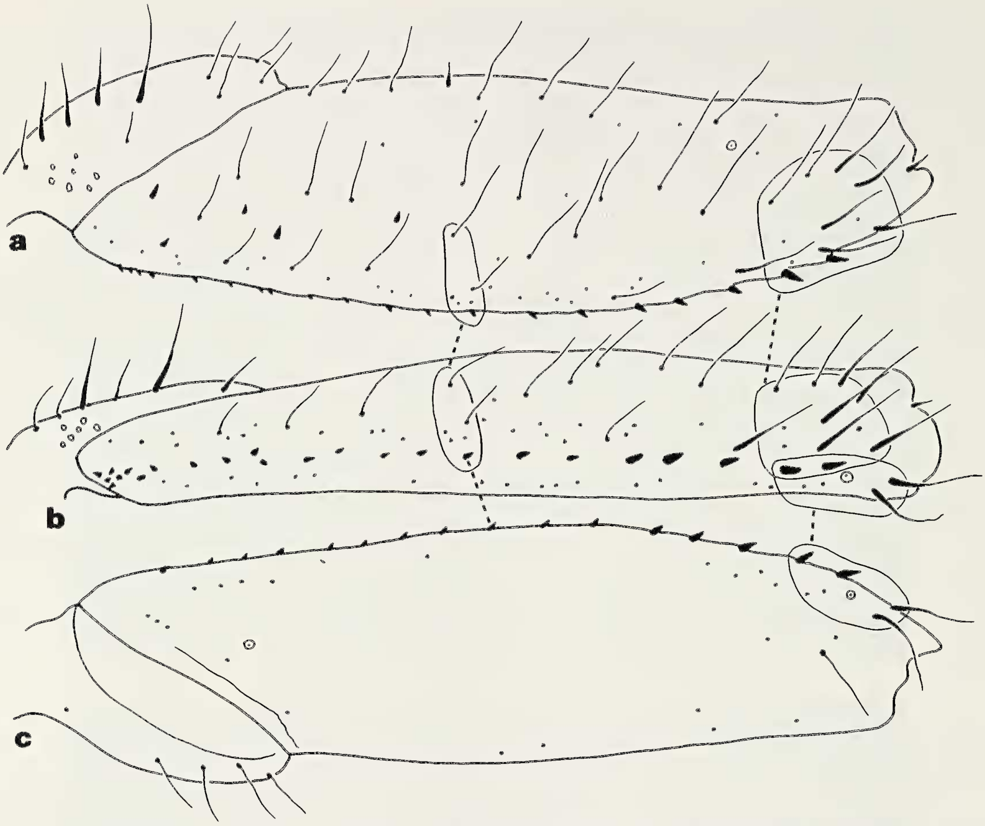


Fig. 7.—*Ochthebius interruptus*, metafemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae indicated by dashes and loops.

workers, and a hypothesis of the function of the hyaline borders has not previously been proposed.

It seems highly likely that the hyaline borders serve as antimicrobial surfaces, and provide spreading surfaces for exocrine gland secretions. The combination of smoothness and flexibility allows the hyaline surfaces to be effectively cleaned of bacteria and debris, and applied with chemicals, while resulting in minimal wear of the surfaces that are rubbed together (the hyaline borders and the scraping setae of the legs), via effective flexibility of the hyaline borders.

The ah- and ph-borders each scrape against opposing, correspondingly smooth surfaces on the head and elytra, respectively. During normal body movements these borders flex and their free margins scrape against the opposing surfaces, preventing bacteria from attaching. The accumulation of bacteria and debris commonly seen on the upper surface of the lh-border is clear evidence of the importance of the hyaline borders to the respiratory system. These hyaline borders may also function in other ways, such as serving as spreading surfaces for pheromones or as evaporative surfaces to aid in the removal of water during grooming.

There seems to be a correspondence between the relative size of the lh-border and the density of the geographical distribution of species. That is, "rare" species with widely disjunct populations often have larger lateral hyaline borders than do

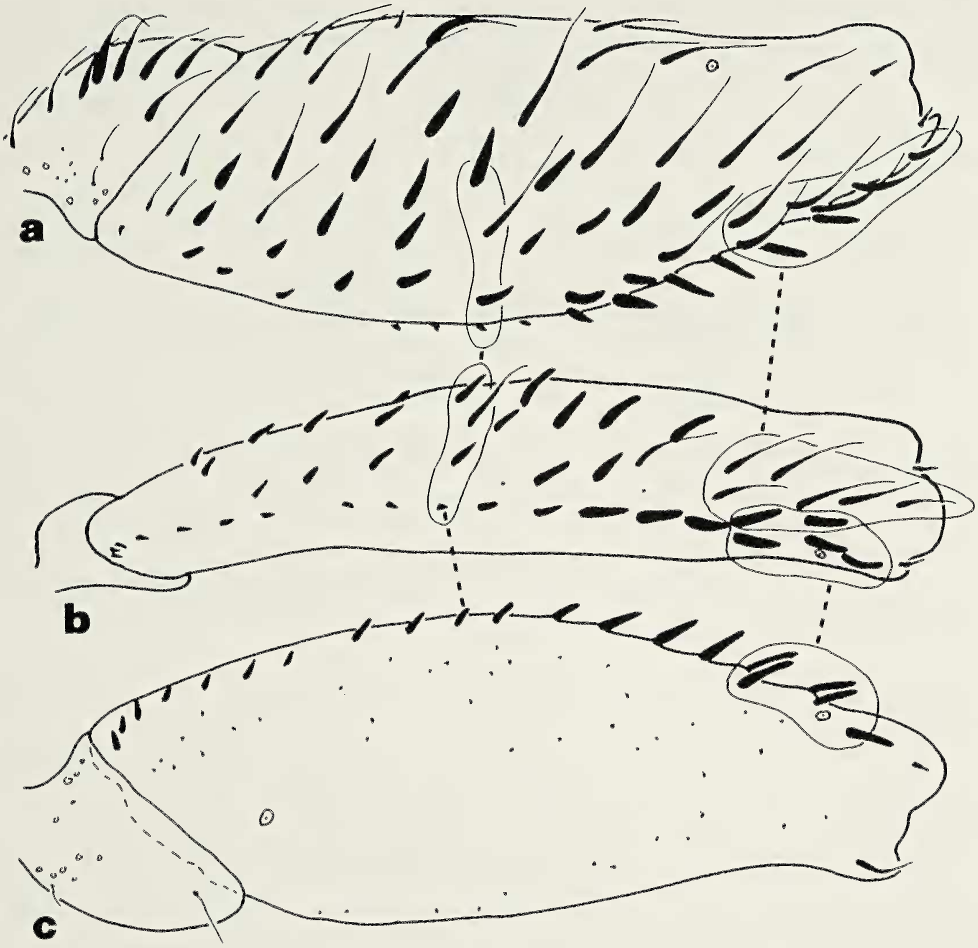


Fig. 8.—*Ochthebius puncticollis,* metafemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae indicated by dashes and loops.

related, more densely populated species. This correspondence needs more study, it may relate to pheromone communication and the evolution of wider hyaline borders.

Derivation of the Hyaline Borders.—Many nonochthebiine Hydraenidae possess an anterior and a posterior hyaline border. This suggests strongly that the ancestral ochthebiine had these structures.

The new genus *Protochthebius* (see description below) has the presumed ancestral condition. A hyaline border is located ventrally at the lateral margin of the hypomeron. Since this hyaline border forms the bubble margin, it is interpreted as being the hh-border, although it is located almost laterally. Unlike the derived hh-border of *Ochthebius,* which is in a vertical plane, the hh-border of *Protochthebius* is oriented in a more horizontal plane and is therefore visible in dorsal aspect, extending slightly beyond the lateral margin of the pronotum. The postocular area lacks both the psd-sulcus and the psd-setae, and the hypomeral an-

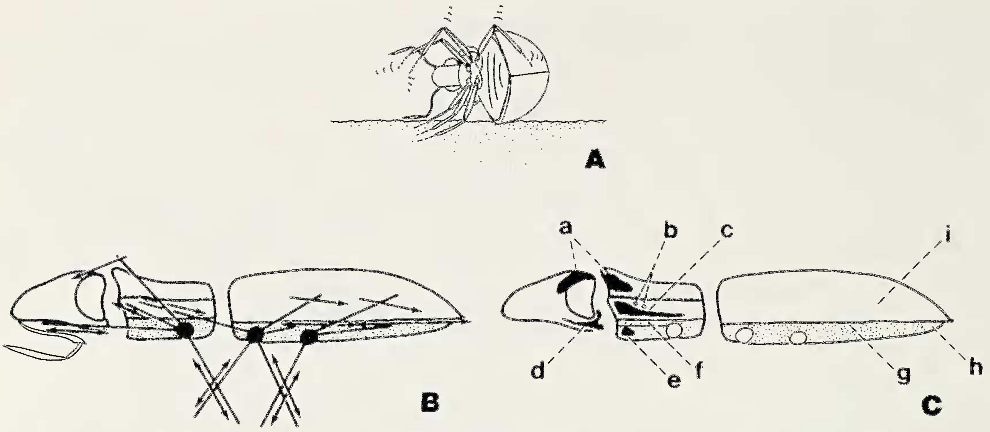


Fig. 9.—*Hydraena americana,* schematic. A. Beetle balanced on edge, the tibiae of the right legs resting on the surface of a wet leaf, the left legs performing secretion-grooming. B. Secretion-grooming movements of left tibiae (note pivotal role of middle leg). C. Locations of exocrine gland pore areas (PA) and sensillar areas (SA): (a) pronotal SA on anterolateral angle, (b) hypomeral dome-shaped sensillar pair, (c) hypomeral PA, (d) postocular and genal PA/SA, (e) prosternal PA, (f) hypomeral exocrine sulcus (PA) for maintaining respiratory bubble, (g) elytral epipleuron (PA), (h) apical abdominal sterna, outside of respiratory bubble (PA), (i) elytral exocrine glands (associated with serial punctures and setae).

tennal pocket setae are absent. The antennal pocket is extremely shallow and entirely pubescent.

The hh-border extends the full length of the hypomeron in the vast majority of species of *Ochthebius.* Only extremely rarely is the posterior part of the hh-border lost without a trace. This loss appears to be associated with the development of extremely wide lh-borders. An example of this is *O. spatulus* (Fig. 32C).

Only very rarely does the prothorax lack the lh-border, while having the other three (for example, an undescribed species from Nepal). Additional study is needed to determine if this indeed represents a primary condition, or results from a secondary loss of the lh-border.

Genus Hydraena

Secretion-Grooming Behavior.—The secretion-grooming behavior of *Hydraena* described below is based on observations of two closely related and very morphologically similar North American species, *H. americana* and *H. vandykei.*

Although the cosmopolitan genus *Hydraena* is quite diverse in body form and dorsal sculpture, the ventral structures involved in secretion-grooming do not show marked differences. Therefore, the behavior described below might reasonably be anticipated in many other (if not all) species of the genus. It remains to be determined whether the modified male protibiae and metatibiae found in many species of the genus relate in some way to differences in secretion-grooming behavior; the two species reported on here do not have sexually dimorphic legs.

At the outset of secretion-grooming, which is performed out of the water, the beetle positions the legs on one side such that the tibiae are resting on a wet surface (such as a partially decomposed leaf). The body is then tilted until the legs on the opposite side are in the air, the body therefore being "on edge" (Fig. 9A).

The "free" legs then begin a process of repeatedly rubbing certain areas of the cuticle with the tibiae (Fig. 9B). As the secretion-grooming progresses, the legs and the parts of the body rubbed by the legs take on a glistening appearance, presumbly due to a coating of the exocrine secretions.

Several of these rubbing actions, especially the remarkable placement of the mesotibia against the hypomeron, are accomplished with the prothorax rotated and angled relative to the pterothorax. This positioning is possible because of the wide intersegmental membrane between the pro- and mesothorax. Located in this membrane are the mesothoracic spiracles; rotation of the prothorax opens this area and exposes the surfaces.

The protibia principally rubs four locations: (1) the anterior part of the bubble-hypomeron, rubbing back and forth along the anterior part of the hypomeral secretion delivery surface and hsd-sulcus (e.g., Fig. 9C:f, 12); (2) the anterior part of the wet-hypomeron, rubbing back and forth in the general area where are located three separate clusters of exocrine pores (Fig. 9C:c, 11B:i, 14B:i); (3) the undersurface of the head, rubbing back and forth, from the genal antennal pocket setae, along the antennal groove beneath the eye, and forward to the lateral process of the mandible (Fig. 9C:d, 20A:b); and (4) the dorsal part of the anterolateral angle of the pronotum, in a sweeping motion forward, first over the anterolateral elongate setae, and then over the top of the eye (Fig. 9C:a).

The mesotibia is extremely interactive, having principally four operations: (1) stroking backward on the elytron, sometimes in unison with the metatibia; (2) mutual rubbing back and forth with the metatibia; (3) similar rubbing with the protibia; and (4) rubbing back and forth on the hypomeron (inserted between the body and the profemur), sometimes stroking the hypomeron in unison with the protibia.

The mesotibia plays a pivotal role in mixing and distributing the glandular secretions, in addition to removing debris and microorganisms. The actions of the middle legs are remarkable for their dexterity and rapidity. Often the mesotibia alternately rubs the protibia and the metatibia; that is, while the protibia is performing its grooming actions on the head and prothorax, the meso- and metatibia are rubbing each other, then the meso- and protibia start mutual rubbing and the metatibia returns to rubbing the elytra. Sometimes the mesotibia, in sequence, rubs the hypomeron, then the protibia, then the metatibia. The mesotibia also rubs all surfaces of the profemur and metafemur. The metatibia repeatedly strokes the side and edge of the elytron, and sometimes strokes the apical abdominal sterna.

Other tibial rubbing observed in specimens in a typical standing position include pro- and mesotibial mutual rubbing, and rubbing of the metatibiae against each other and against the apical sterna.

ESDS Cuticular Components.—In contrast to the ESDS of *Ochthebius,* in *Hydraena* the concentration of exocrine glands associated with the bubble margin are located in the prothorax. Although the postocular area of *Hydraena* is complex (see below), there is no exocrine gland system similar to that of *Ochthebius.* The antennal pocket is formed differently than that of *Ochthebius,* and contains an antennal cleaner, a structure not present in *Ochthebius.*

Hypomeral Secretion Delivery Sulcus.—The pores of exocrine glands associated with the bubble margin lie in a longitudinal groove, the hypomeral secretion delivery (hsd-) sulcus (g in Fig. 10B; 12A, B; and 14A). The hsd-sulcus is extremely narrow, and in some groups is not visible (even with SEM) unless the specimen is treated with potassium hydroxide (to remove the smooth secretion

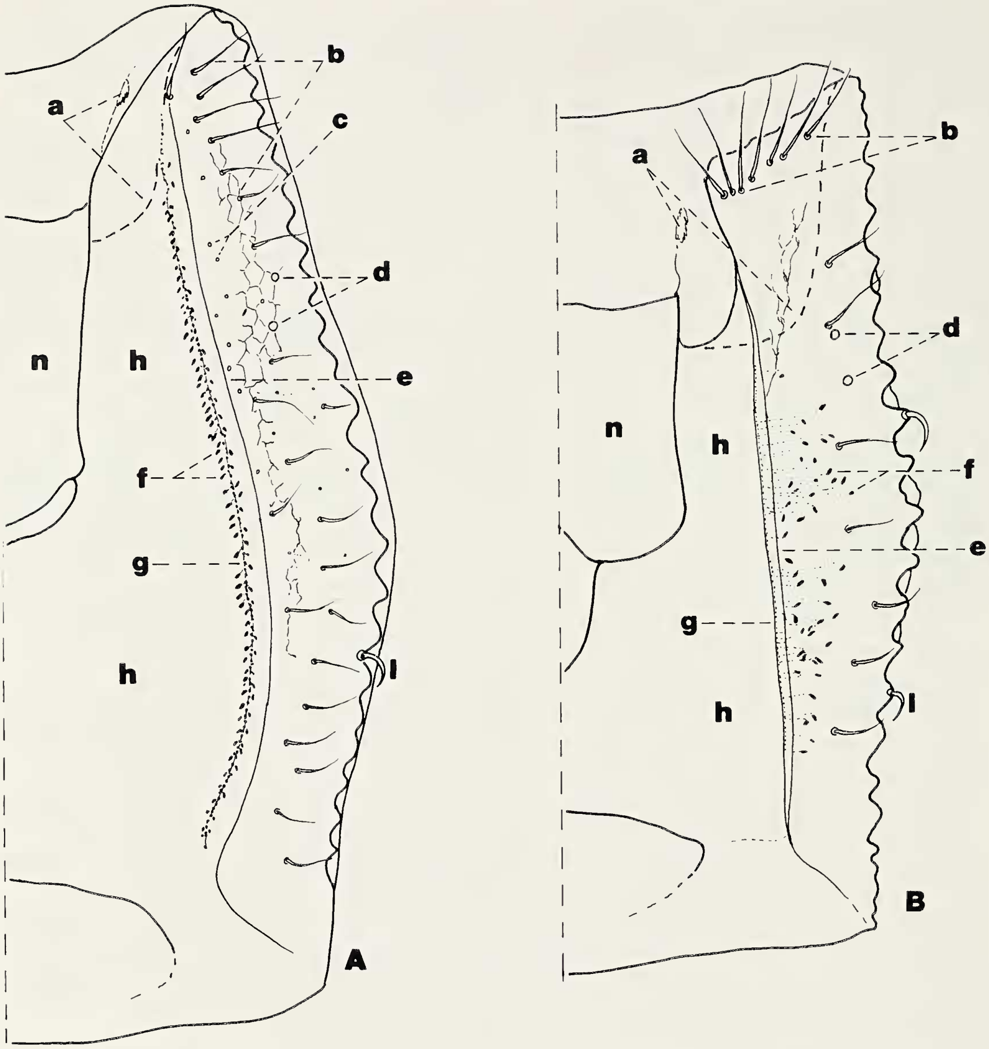


Fig. 10.—*Hydraena*, venter of left side of prothorax. A. *H. gracilis*. B. *H. testacea*. Structures: (a) antennal cleaner and antennal pocket, (b) hap-setae, (c) exocrine pores of wet-hypomeron, (d) hypomeral dome-shaped sensillar pair, (e) hsd-carina, (f) end-apparatus and ductules of exocrine glands, (g) hsd-sulcus on hsd-surface, (h) hydrofuge hypomeron, (l) lateral seta, (n) prosternum.

filling the sulcus). It is possible that, in some groups, part of the sulcus is closed, forming a tube that delivers the secretion toward the antennal pocket (see Fig. 13B); incisive histological study is needed to clarify this.

The hsd-sulcus is located on a relatively smooth and raised surface, the hypomeral secretion delivery (hsd-) surface. In the subgenus *Haenydra* (e.g., *gracilis*) the hsd-surface (Fig. 13A:g, 14A:g) is flat, completely smooth, and equally wide on both sides of the hsd-sulcus. In other groups (e.g., the nominate subgenus) the hsd-surface is slightly convex, and the hsd-sulcus lies along the medial margin of this ridge, the hsd-surface between the hydrofuge area and the hsd-sulcus being comparatively narrow (e.g., *riparia*; Fig. 12A, B). In still other groups (e.g., the

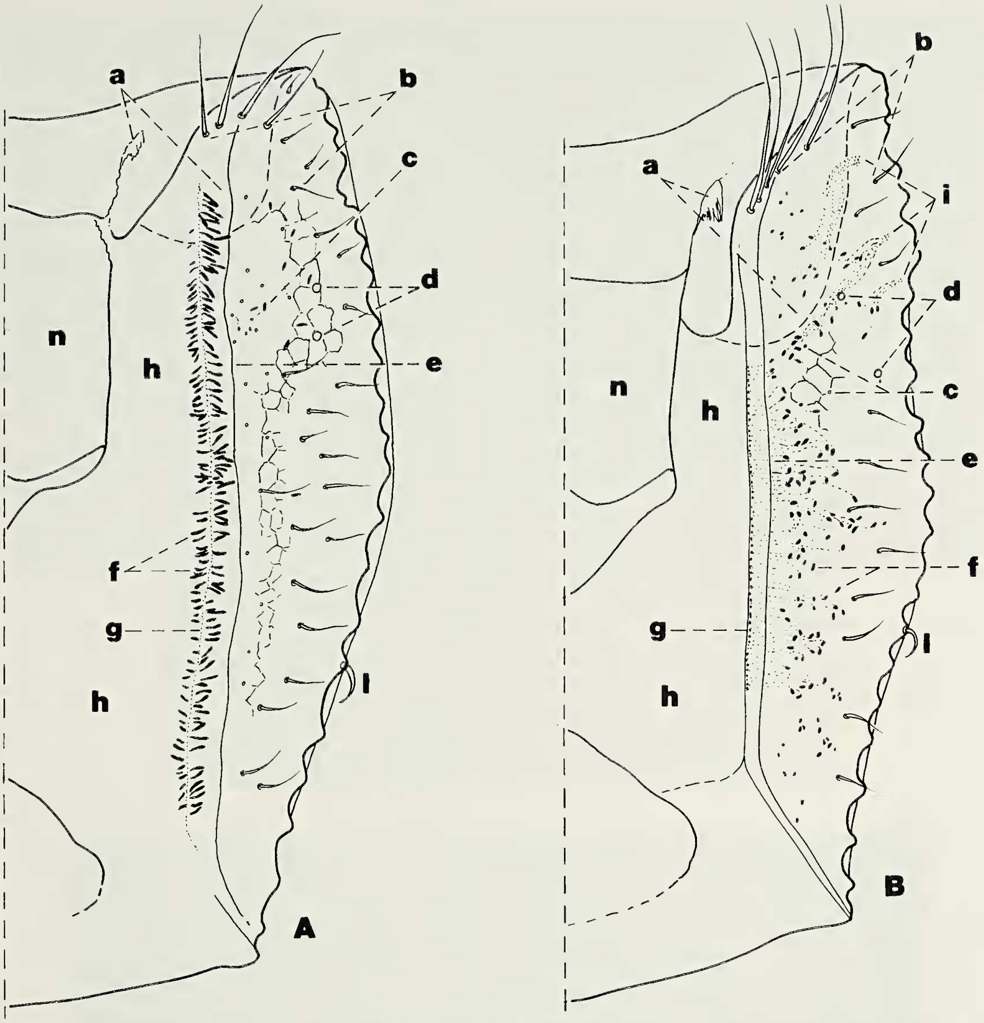


Fig. 11.—*Hydraena*, venter of left side of prothorax. A. *H. riparia*. B. *H. americana*. Structures: (a) antennal cleaner and antennal pocket, (b) hap-setae, (c) exocrine pores of wet-hypomeron, (d) hypomeral dome-shaped sensillar pair, (e) hsd-carina, (f) end-apparatus and ductules of exocrine glands, (g) hsd-sulcus on hsd-surface, (h) hydrofuge hypomeron, (i) exocrine pore clusters of wet-hypomeron, (l) lateral seta, (n) prosternum.

subgenus *Phothydraena*) the hydrofuge surface is contiguous with the hsd-sulcus, the latter lying along the medial margin of the quite convex (nearly cariniform) hsd-surface (e.g., *testacea*; Fig. 18A:g). The hsd-surface terminates laterally in the hypomeral secretion delivery (hsd-) carina, a sharp cuticular ridge that forms the lateral boundary of the bubble-hypomeron.

Antennal Pocket and Antennal Cleaner.—The antennal pocket is well formed and has, at its anteromedian extreme, a well-defined cluster of specialized spines that is here interpreted, based on location and shape, to be an antennal cleaning device. The antennal cleaner varies among the species groups in the degree of clustering of the spines. For example, the spines are densely clustered in *Hydraena*

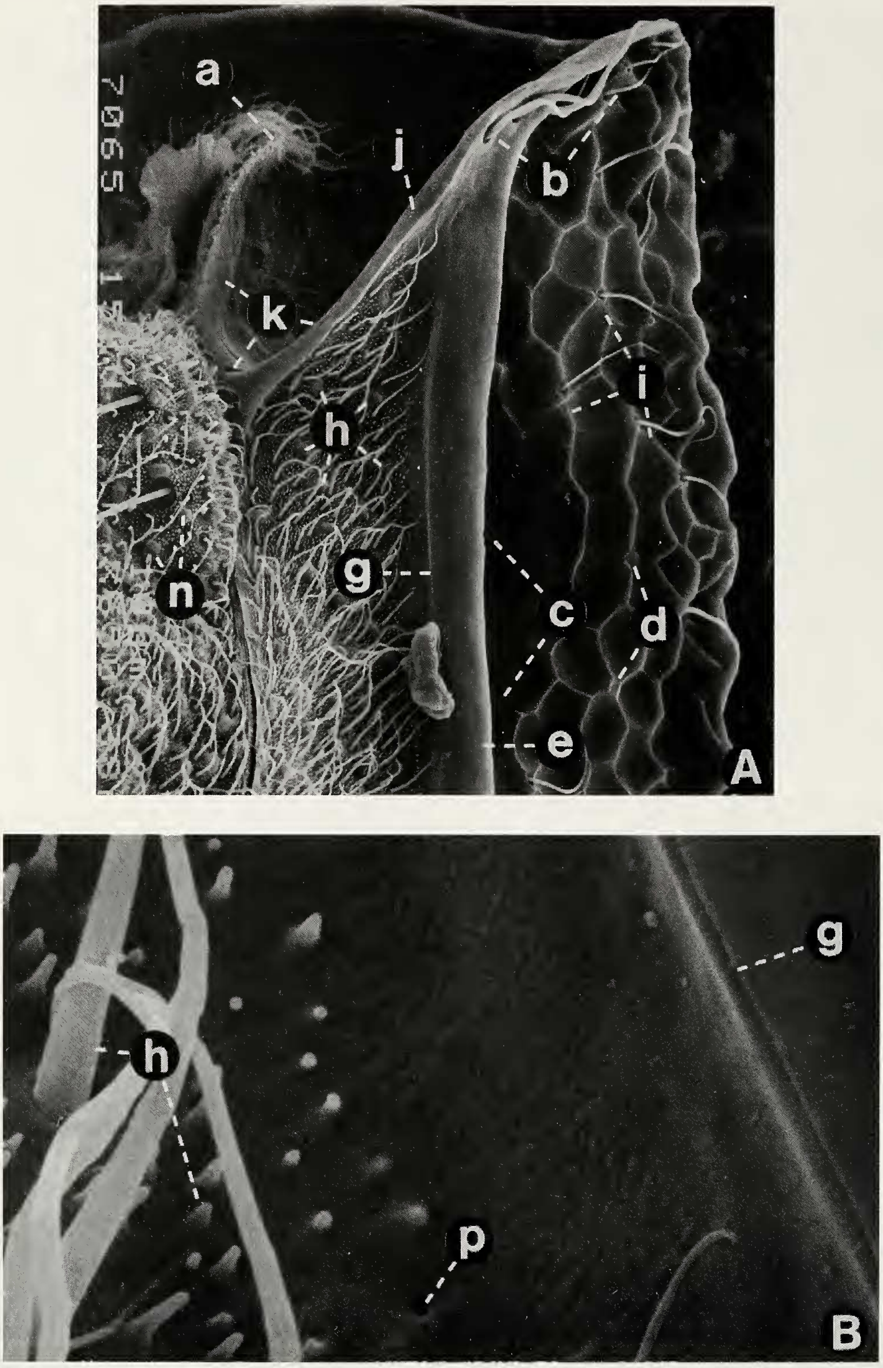


Fig. 12.—*Hydraena riparia*. A. Hypomeron, anterior aspect of left side. B. Detail of exocrine sulcus (g) and adjacent hydrofuge. Structures: (a) antennal cleaner, (b) hap-setae, (c) exocrine pores of wet-hypomeron, (d) hypomeral dome-shaped sensillar pair, (e) hsd-carina, (g) hsd-sulcus on hsd-surface, (h) asperite hydrofuge hypomeron and (in A) secretions, (i) exocrine pore clusters of wet-hypomeron, (j) marginal asperites of antennal pocket, (k) marginal pores of antennal pocket, (n) prosternum, (p) exocrine pore of hydrofuge hypomeron.

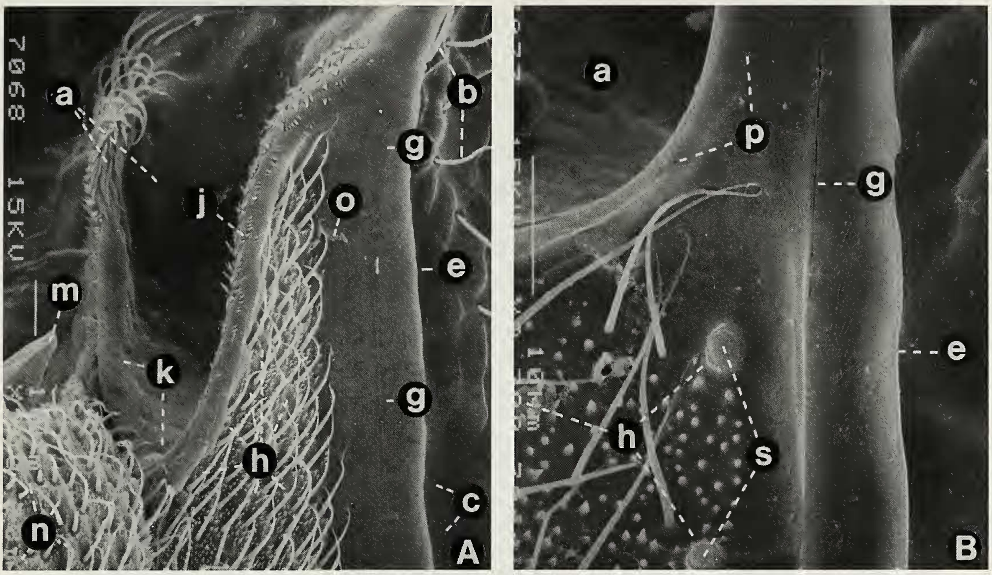


Fig. 13.—*Hydraena,* hypomeron and antennal pocket. A. *H. gracilis,* anterior aspect of left side. B. *H. americana,* detail of exocrine sulcus (g) and adjacent asperite hydrofuge. Structures: (a) antennal cleaner and antennal pocket, (b) hap-setae, (c) exocrine pores of wet-hypomeron, (e) hsd-carina, (g) hsd-sulcus on hsd-surface, (h) exocrine pores in asperite hydrofuge hypomeron, (j) marginal asperites of antennal pocket, (k) marginal pores of antennal pocket, (m) cervical sclerite, (n) prosternum, (o) bacteria, (p) marginal pores of antennal pocket, (s) secretion "caps" of exocrine pores.

"new species A" (Fig. 15B, 16D) and *H. americana* (Fig. 17A, B), but less densely clustered in *H. testacea* (Fig. 16A, B), *H. riparia* (Fig. 16C), and *H. gracilis* (Fig. 17C, D).

Associated with the antennal cleaner is a bottle-shaped sensillum, located more toward the "head side" of the antennal cleaner (Fig. 15B:s; 16:b; 17:b), asperite hydrofuge pubescence (e.g., Fig. 16A:h), and exocrine pores of the antennal pocket (e.g., Fig. 16A:p). The antennal pocket has exocrine pores near the posterior margin (k in Fig. 12, 13, and 18), and often has sharp, tiny asperites on its lateral margin (j in Fig. 12 and 13).

Hypomeral Hydrofuge.—The bubble-hypomeron posterior to the antennal pocket is clothed in asperite hydrofuge consisting of flagelliform setae and much smaller, denser asperites (the prosternum has similar asperite hydrofuge). The shapes, sizes, and density of the flagelliform setae and (especially) the asperites vary among the species groups (h in Fig. 12–14).

Interspersed in the asperite hydrofuge are single exocrine pores. In many groups each pore is surrounded by tiny asperites to form an exocrine pore crown (h in Fig. 13B and 18C, D). In some SEM preparations, a secretion cap can be seen covering the pore crown (s in Fig. 13B and 18C [cap dislodged from its crown]).

Structures of the Wet-hypomeron.—Hypomeral antennal pocket (hap-) setae, usually seven in number, are located near the margin of the antennal pocket (b in Fig. 10–13 and 18; Fig. 19:m). (These setae are not homologous with the hap-setae of *Ochthebius.*) The locations of the hap-setae vary among the species groups.

In all species studied, hypomeral paired (hp-) sensilla (d in Fig. 10–12 and 18)

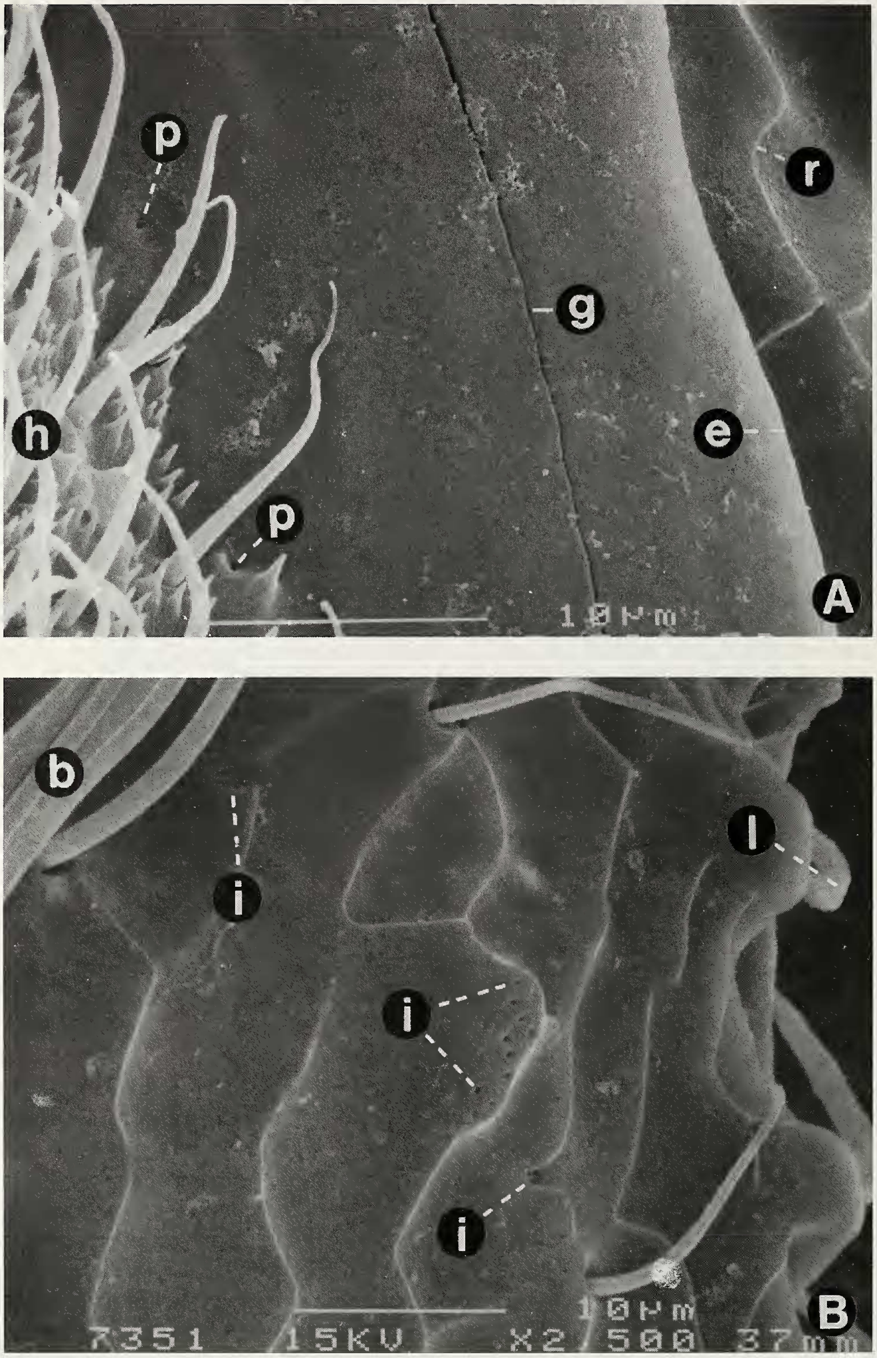


Fig. 14.—*Hydraena*, hypomeron, left side. A. *H. gracilis*, exocrine sulcus (g) and adjacent asperite hydrofuge. B. *H. americana*, anterior aspect of wet-hypomeron. Structures: (b) hap-setae, (e) hsd-carina, (g) hsd-sulcus on hsd-surface, (h) asperite hydrofuge, (i) exocrine pore clusters of wet-hypomeron, (l) lateral seta, (p) exocrine pores in asperite hydrofuge hypomeron, (r) microreticulation.

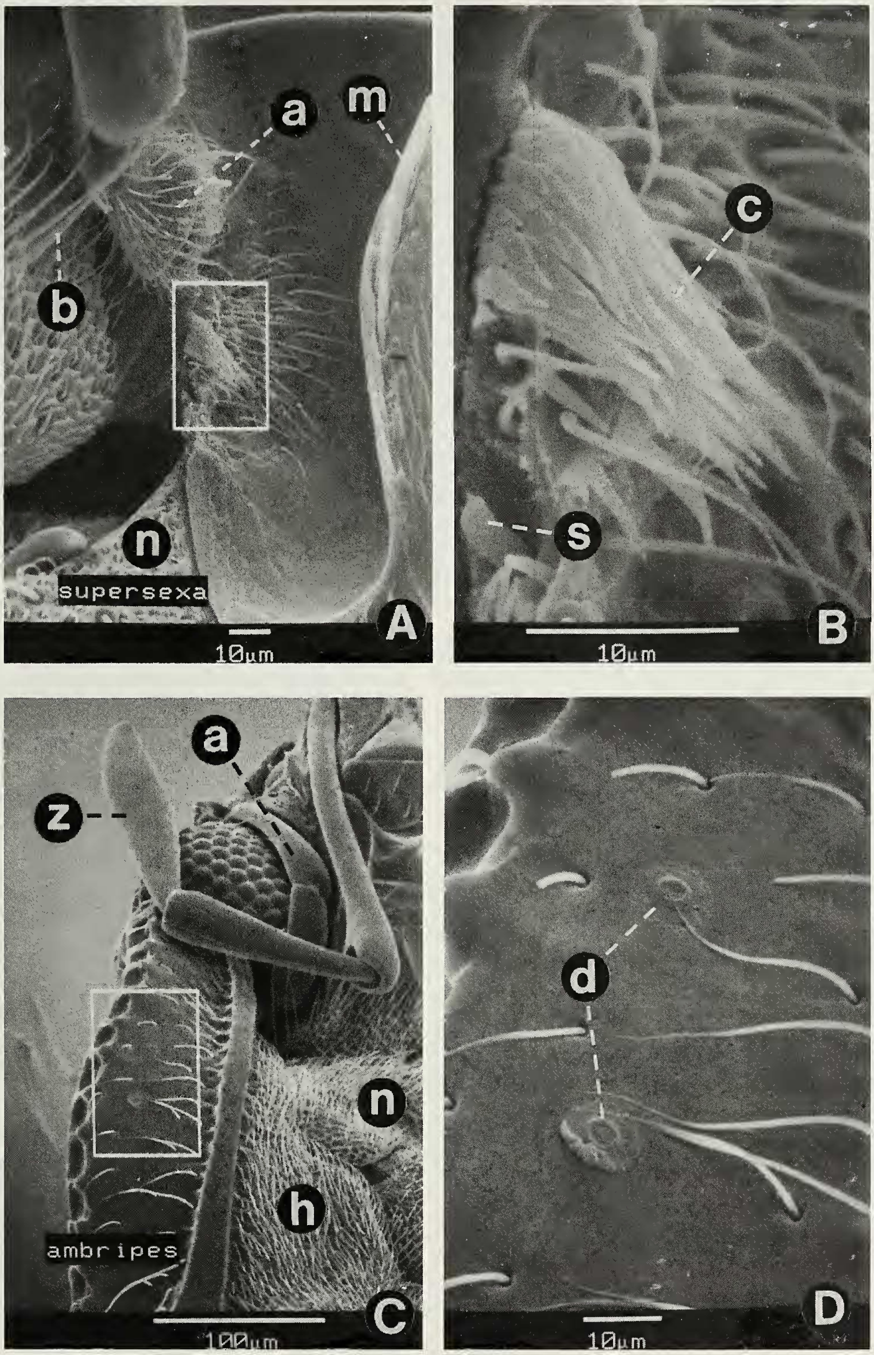


Fig. 15.—*Hydraena* (undescribed species from Papua New Guinea). A. Species "S," postocular area and antennal pocket. B. Rectangular area of A, enlarged. C. Species "A," hypomeron, right side. D. Rectangular area of C, enlarged. Structures: (a) antenna, (b) gap-setae, (c) antennal cleaner, (d) dome sensillar pair of wet-hypomeron, (h) hydrofuge hypomeron, (m) antennal pocket setae, (n) prosternum, (s) bottle-shaped sensillum, (z) maxillary palpus.

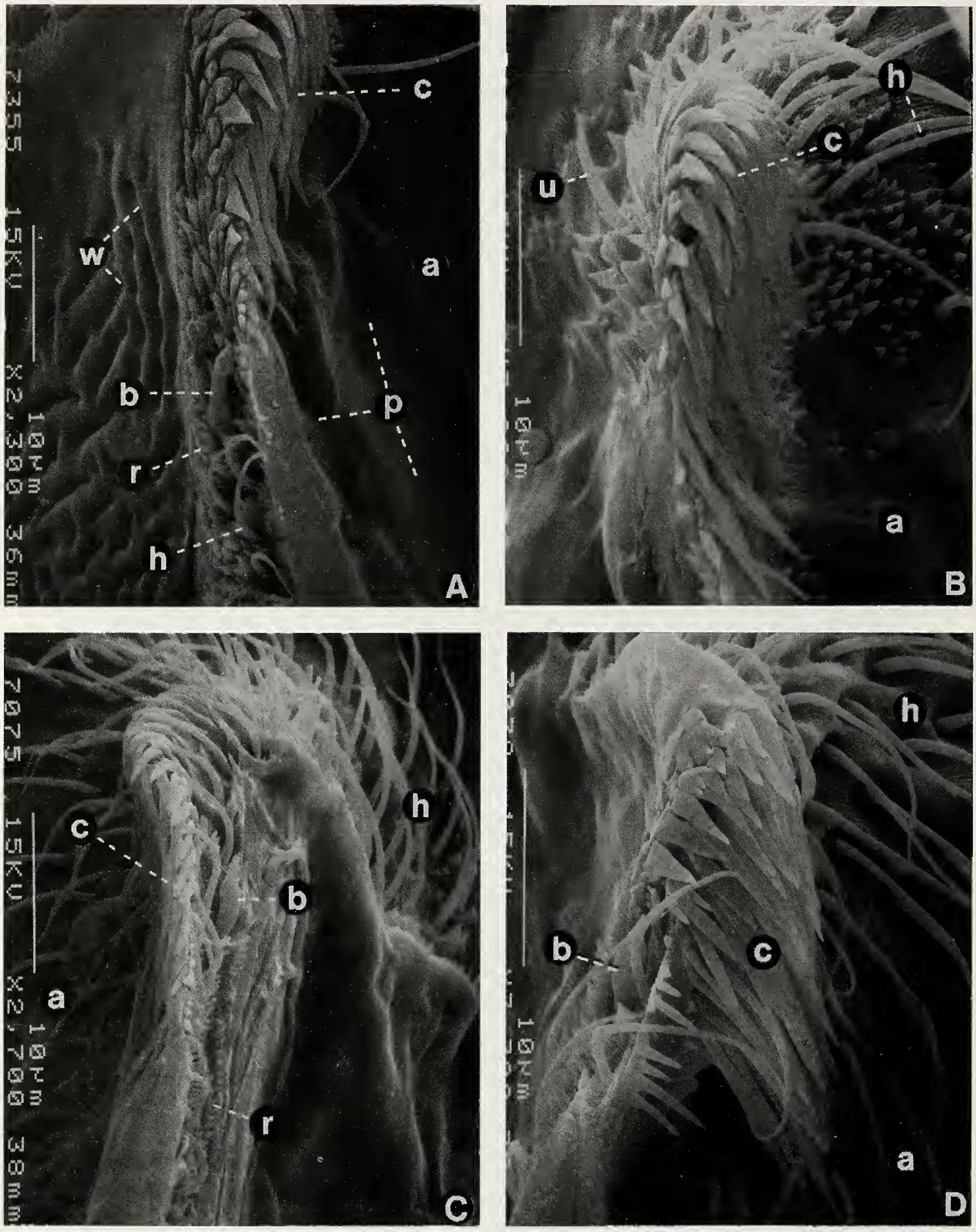


Fig. 16.—*Hydraena,* antennal cleaners. A, B. *H. testacea.* C. *H. riparia.* D. Undescribed species "S," Papua New Guinea. Structures: (a) antennal pocket, (b) bottle-shaped sensillum, (c) antennal cleaner, (h) asperite hydrofuge pubescence, (p) exocrine pores of antennal pocket, (r) asperites of antennal pocket margin, (u) sensillum(?), (w) cuticular wrinkles.

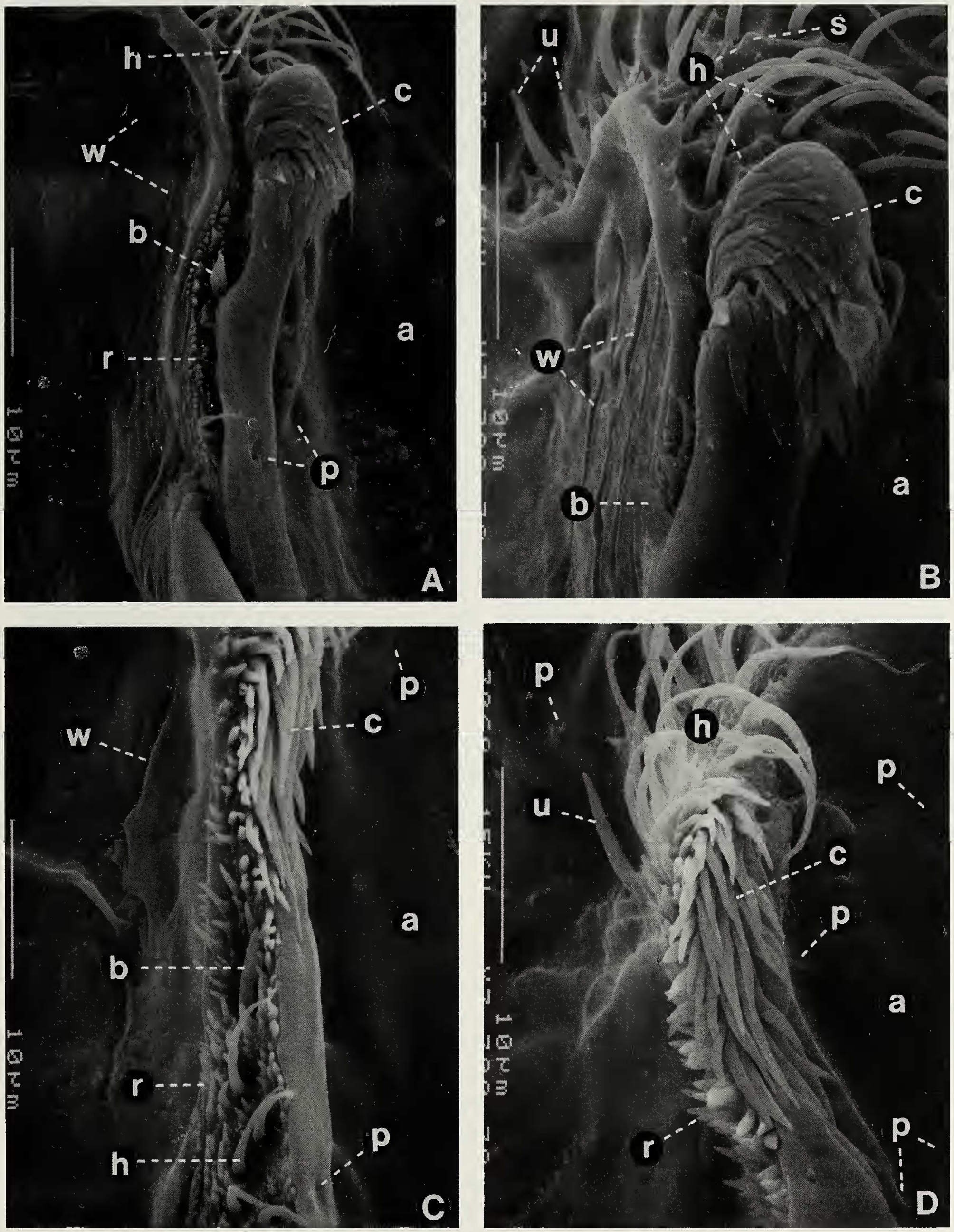


Fig. 17.—*Hydraena,* antennal cleaners. A, B. *H. americana.* C, D. *H. gracilis.* Structures: (a) antennal pocket, (b) bottle-shaped sensillum, (c) antennal cleaner, (h) asperite hydrofuge pubescence (exocrine pores indicated in A and B, (p) exocrine pores of antennal pocket, (r) asperites of antennal pocket margin, (s) secretion "cap" on exocrine pore in hydrofuge area, (u) sensilla(?), (w) cuticular wrinkles.

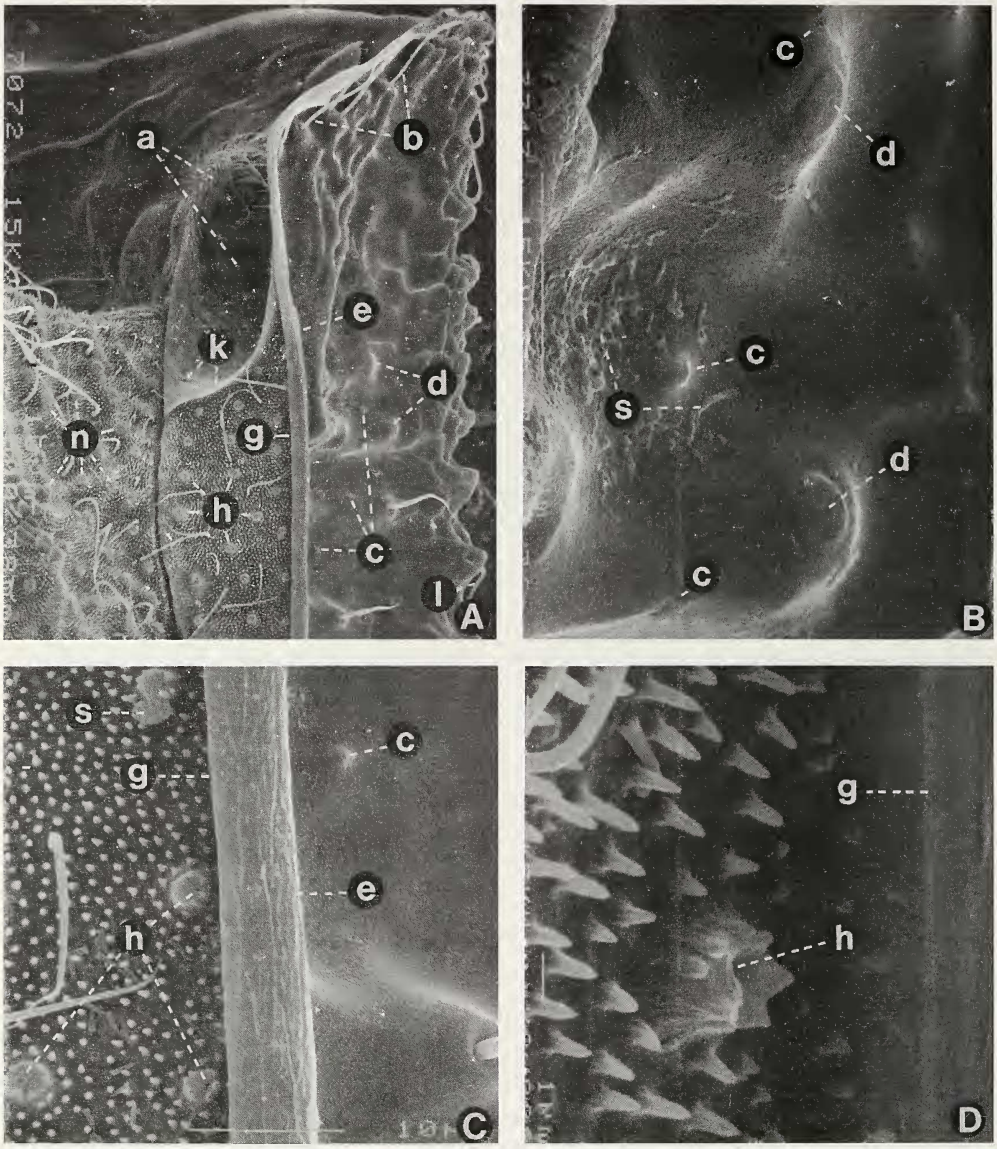


Fig. 18.—*Hydraena testacea,* hypomeron. A. Anterior aspect of left side. B. Detail of dome-sensilla. C. Detail of hypomeral carina and adjacent structures. D. Detail of exocrine sulcus. Structures: (a) antennal cleaner and antennal pocket, (b) hap-setae, (c) exocrine pores of wet-hypomeron, (d) hypomeral dome-shaped sensillar pair, (e) hsd-carina, (g) hsd-sulcus on hsd-surface, (h) exocrine pore "crowns" of asperite hydrofuge hypomeron, (k) marginal pores of antennal pocket, (l) lateral seta, (n) exocrine pore "crowns" of prosternum, (s) presumed exocrine secretion.

are located in the anterior half of the wet-hypomeron, approximately opposite the prosternum. These structures are tiny pits with a thin cuticular cover having a minute central pore (Fig. 18B:d). Histological study will probably show the hp-sensilla to be chemoreceptive coeloconic sensilla (consisting of a sensory peg

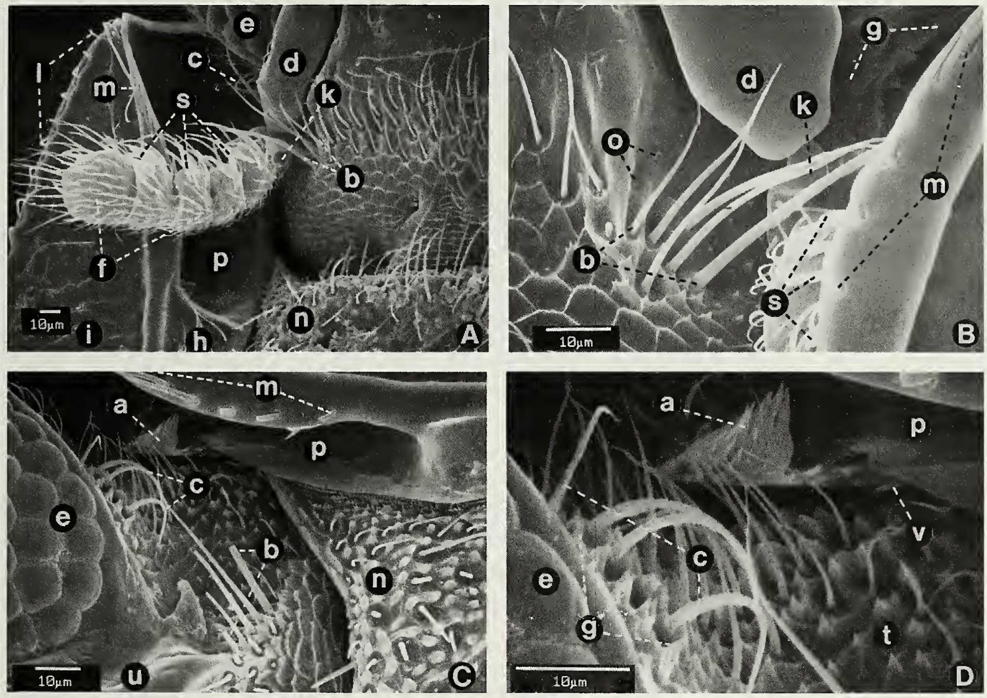


Fig. 19.—*Hydraena* (undescribed species from Papua New Guinea), postocular area and antennal pocket. A. Species "THO," right side, antennal club. B. Species "R," left side, gena and antenna. C, D. Species "Q," left side. Structures: (a) antennal cleaner, (b) gap-setae, (c) postocular setae, (d) second antennomere, (e) eye, (f) antennal hydrofuge pubescence, (g) postocular peg sensilla, (h) hydrofuge hypomeron, (i) wet-hypomeron, (k) cupule article of antenna, (l) lateral setae, (m) antennal pocket setae, (n) prosternum, (o) exocrine pores, (p) antennal pocket, (s) sensilla of antennal club, (t) genal asperite hydrofuge, (u) subocular antennal groove, (v) bottle-shaped sensillum.

in a fluid-filled cavity). In one SEM preparation (Fig. 15D:d), the hp-sensilla are covered with a secretion residue.

Single exocrine pores (c in Fig. 10A and 11A, B) are located on the wet-hypomeron, often more closely spaced together (but not clustered) on the area medial to the pair of chemosensilla. In some species, exocrine pore clusters (Fig. 11B:i, 14B:i) are located in the anterior part of the wet-hypomeron.

Sub- and Postocular Antennal Grooves.—In repose, the antenna is held beneath and behind the eye. The first two antennomeres are held beneath the eye, in the subocular antennal (sa-) groove. The sa-groove is usually weakly sculptured (e.g., Fig. 20A; 21A, C).

The postocular and genal areas are separated by the postocular antennal (pa-) groove (Fig. 20:a, 21:a), which is continuous with the sa-groove. The pa-groove is smooth or at most very finely microreticulate, in contrast to the strongly sculptured and setose areas it separates.

When the antenna is held in repose, the antennomeres in contact with the smooth pa-groove are the second (its distal part), the third (a tiny intermediate article), the fourth (the cupule), and perhaps the basal part of the fifth (the first article of the pubescent club; Fig. 19A, B). Therefore, these articles are in a position such that, when the antenna is raised during air capture, the articles would

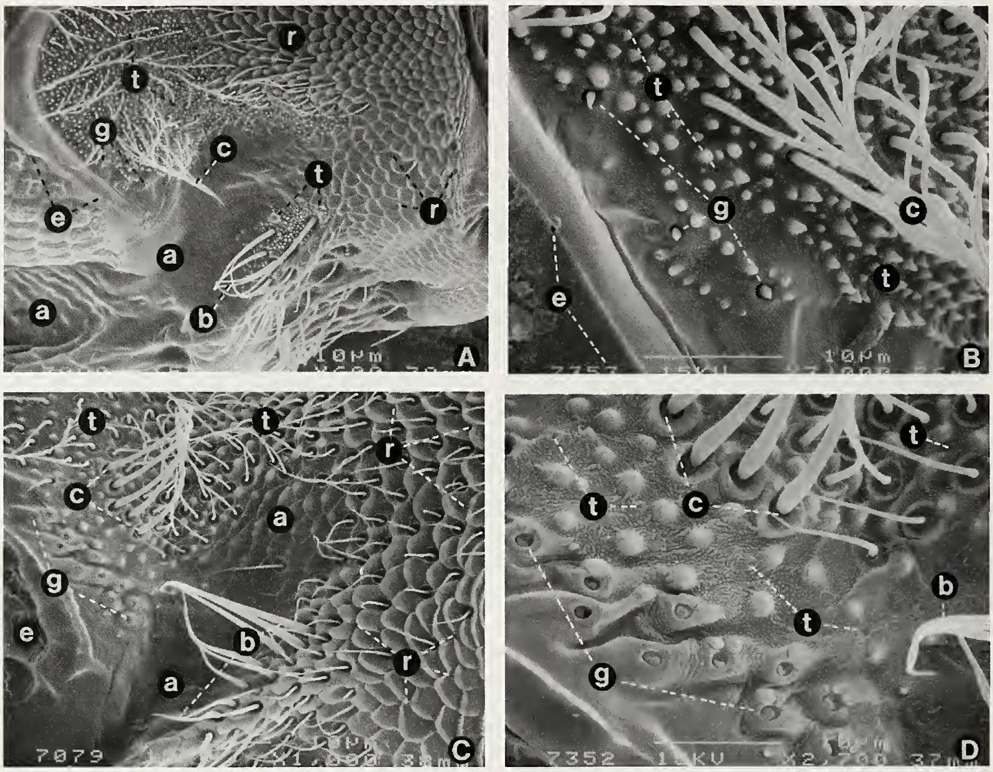


Fig. 20.—*Hydraena,* sub- and postocular areas. A. *H. testacea.* B. Same, detail of peg sensilla area. C. Undescribed species "S" (Papua New Guinea). D. Same, detail of peg sensilla area. Structures: (a) sub- and postocular antennal groove, (b) gap-setae, (c) postocular sensory setae, (e) eye and periocular exocrine pores, (g) postocular peg sensilla, (r) exocrine pores of reticulate hydrofuge, (t) exocrine pores of asperite hydrofuge.

stroke against (or at least nearly touch) the sensilla and setae at the posteroventral angle of the eye.

Because of the flexibility of the antenna at the cupule, the other articles of the pubescent club (articles 6–9) may also be able to stroke against the postocular sensilla and setae when the antenna is raised during air capture.

Postocular Structures.—Six kinds of cuticular microstructures are located in the postocular area: peg sensilla, grooved sensilla, asperites, asperite hydrofuge, reticulate hydrofuge, and exocrine pores.

Peg sensilla (Fig. 19D:g, 20:g) are located adjacent to the orbit of the eye (behind the posteroventral angle of the eye). The amount and density of the peg sensilla, and particulars of the cuticular topography surrounding them, vary among the species groups.

Grooved sensilla (c in Fig. 19, 20, 21D) form a distinct cluster slightly separated from the peg sensilla. These setae are almost certainly chemoreceptors—fractured sensilla appear to have a central lumen (Fig. 21B). These sensilla appear to be articulated at their bases (i.e., sensilla chaetica), although varying from tightly articulated in some groups (Fig. 20B; 21B, D) to having a wide cup-like base indicating a wide range of setal motion (Fig. 20C, D:c).

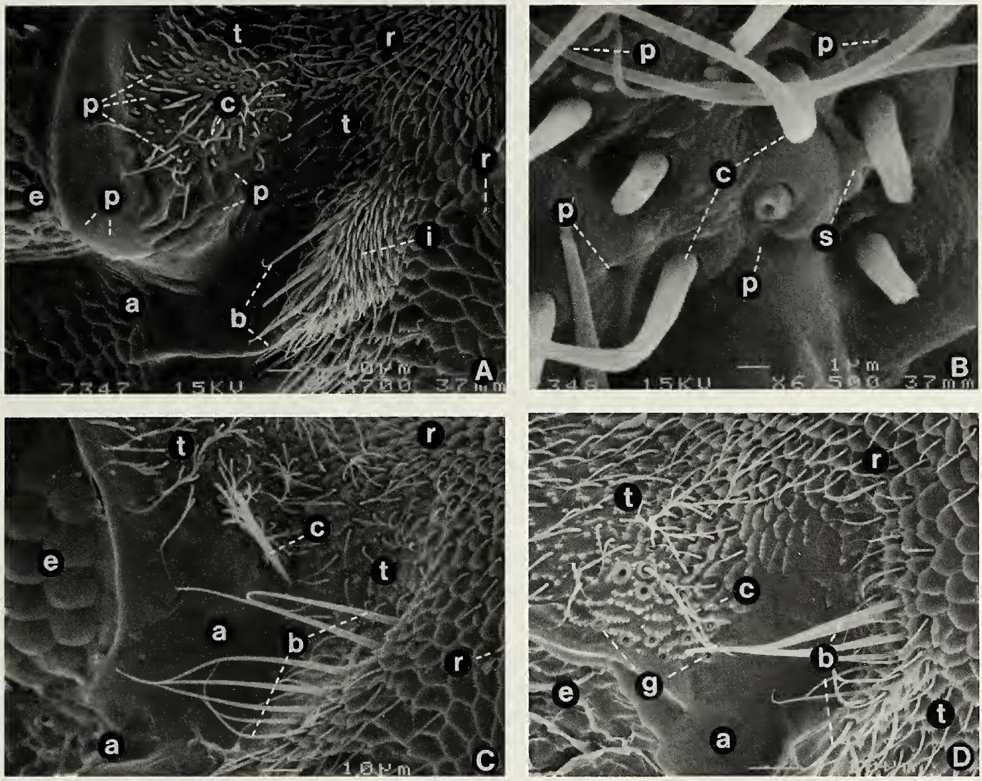


Fig. 21.—*Hydraena,* sub- and postocular areas. A. *H. gracilis.* B. Same, detail of postocular grooved sensory setae. C. *H. riparia.* D. Undescribed species "THU" (Papua New Guinea). Structures: (a) sub- and postocular antennal groove, (b) gap-setae, (c) postocular sensory setae (grooved in B), (e) eye, (g) postocular peg sensilla, (i) genal spiculate area, (p) exocrine pores, (r) reticulate hydrofuge (peg sensillum in A and C), (s) presumed exocrine secretion, (t) asperite hydrofuge.

Asperites, tiny cone-shaped tubercles (Fig. 20:t), are present between and among the peg sensilla and grooved sensilla. In some species the asperites form short linear groups (e.g., Fig. 21D).

In all species, at least part of the postocular area has hydrofuge hairs, varying in density depending upon the species group. In some species the ground microsculpture of the hydrofuge area consists of asperites, forming asperite hydrofuge (e.g., Fig. 20:t). Alternatively, the ground sculpture can consist of microreticulation, forming reticulate hydrofuge (e.g., Fig. 20:r). Exocrine pores (unclustered) are located in various parts of the postocular area (Fig. 20:t, 21B:p).

Genal Structures.—A cluster of long, stiff, tapering setae, the genal antennal pocket (gap-) setae (b in Fig. 19, 20, and 21), are positioned such that, when the antenna is in repose, the gap-setae cover and protect the third, fourth (cupule), and distal portion of the second antennomere. These pivotal antennomeres are the smallest, and presumably the most susceptible to breakage. The cuticular ground sculpture at the gap-setae is asperite, varying from weakly (Fig. 20A), to moderately strongly (Fig. 19B; 20C; 21C, D), to very strongly developed (spiniform; Fig. 21A).

The gap-setae and spiniform asperites probably act as combs that, in addition

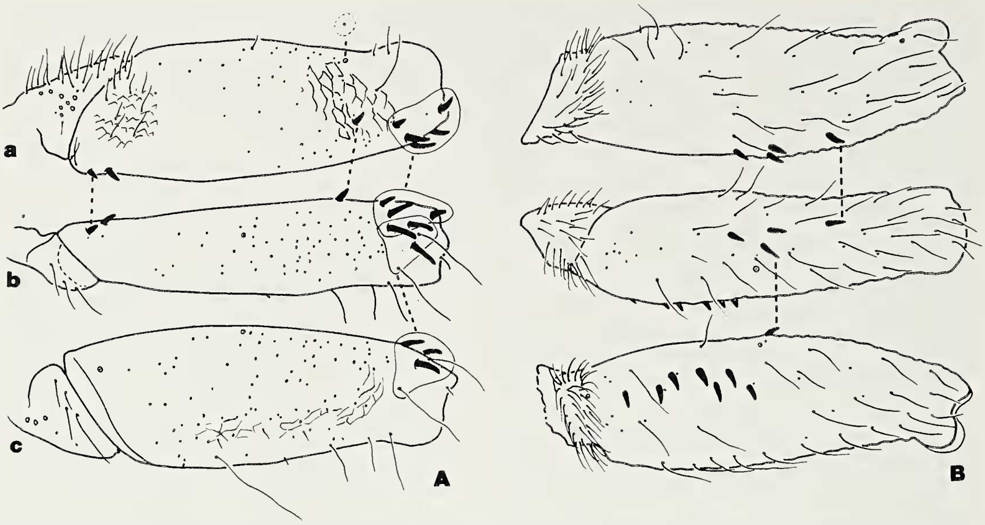


Fig. 22.—Profemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae of distal spine cluster indicated by dashes and loops. A. *Limnebius piceus*. B. *Hydraena americana*.

to the antennal cleaner of the prothorax, clean the pubescent antennal club as it moves in and out of the antennal pocket. Reticulate hydrofuge or asperite hydrofuge is located medial to the gap-setae (Fig. 19A). In some preparations, exocrine pores are visible near bases of the gap-setae (e.g., Fig. 19B:o).

Femoral Setae.—The femora of *H. americana* (Fig. 22B, 23B, 24B) bear many elongate and flexible setae, and few short, stout setae. The locations of the stout setae, on the "facing" surfaces of the pro- and mesofemora, correspond with the mutual rubbing that occurs during secretion grooming.

The lack of distal spine clusters on the femora (see *Ochthebius*) reflects the

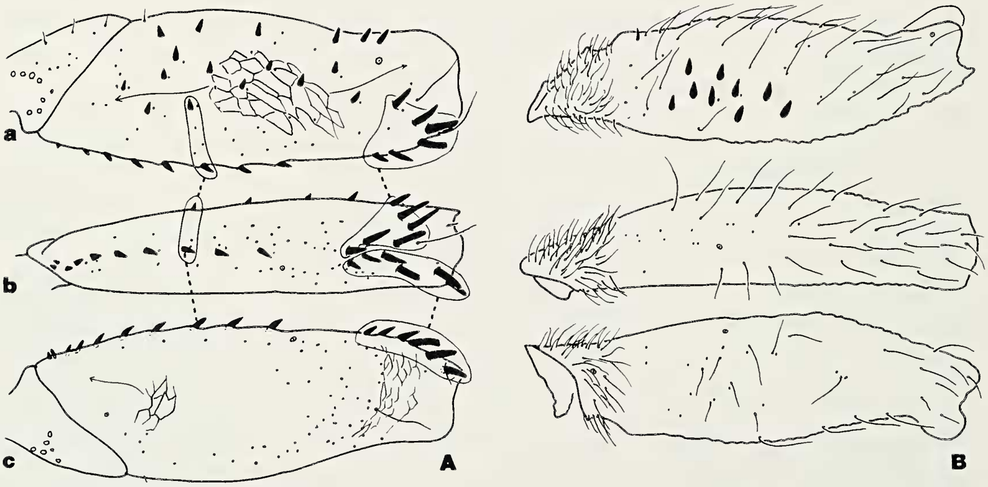


Fig. 23.—Mesofemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae of distal spine cluster indicated by dashes and loops. A. *Limnebius piceus*. B. *Hydraena americana*.

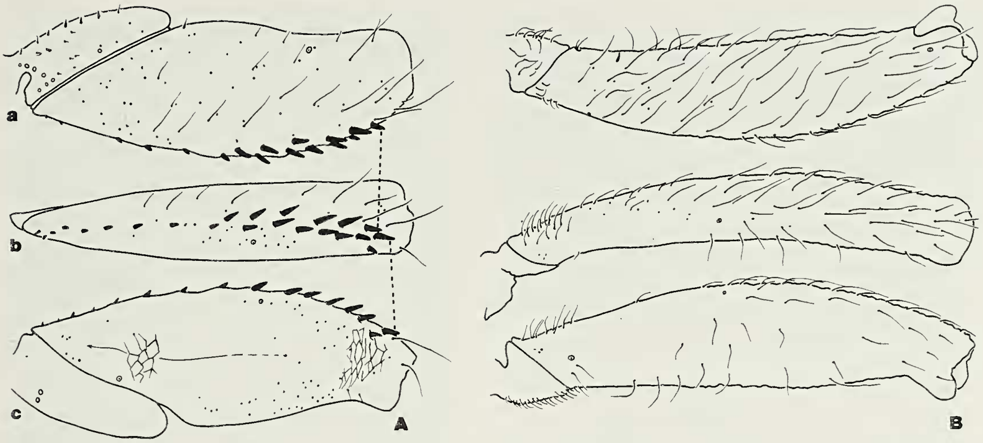


Fig. 24.—Metafemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae indicated by dashes. A. *Limnebius piceus.* B. *Hydraena americana.*

fact that during secretion-grooming it is the tibiae, not the distal part of the femora, that rub other body parts.

Genus Limnebius

Secretion-grooming Behavior.—The secretion-grooming behavior of *Limnebius* described below is based on observations of *L. piceus,* a species from western North America. Aspects of the habitat preferences of the genus and the taxonomy of this species are given by Perkins (1976, 1981).

Although nearly cosmopolitan in distribution, with many species, the genus *Limnebius* is extremely uniform in morphology. I have examined representatives of several species, including some near the size extremes (i.e., the largest and smallest) and species from several geographic regions. All of these species are similar in the presence of the hypomeral glandular fovea (i in Fig. 26C and 27A, B) and the associated exocrine gland cluster (Fig. 26C:j), and similar in most other ventral and leg features (described below).

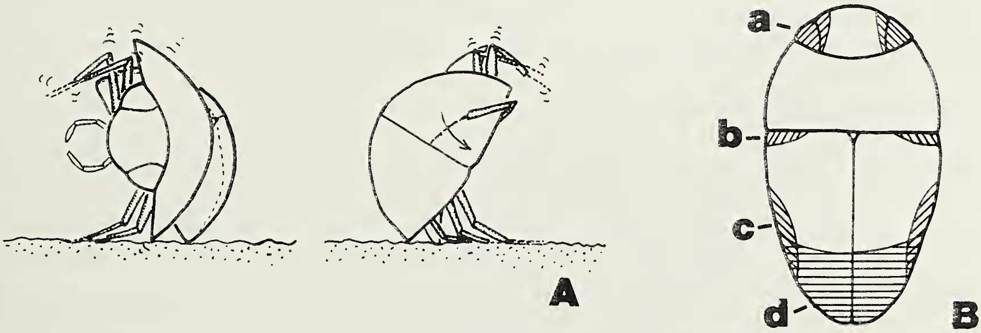


Fig. 25.—*Limnebius piceus,* schematic. A. Beetle balanced on edge, the tibiae of the left legs resting on the surface of a wet leaf, the right legs performing secretion-grooming, anterior (left) and posterior aspects. B. Dorsal areas groomed by legs: (a) protibia and protarsus, (b) protibia, (c) mesotibia, (d) metatibia and metatarsus.

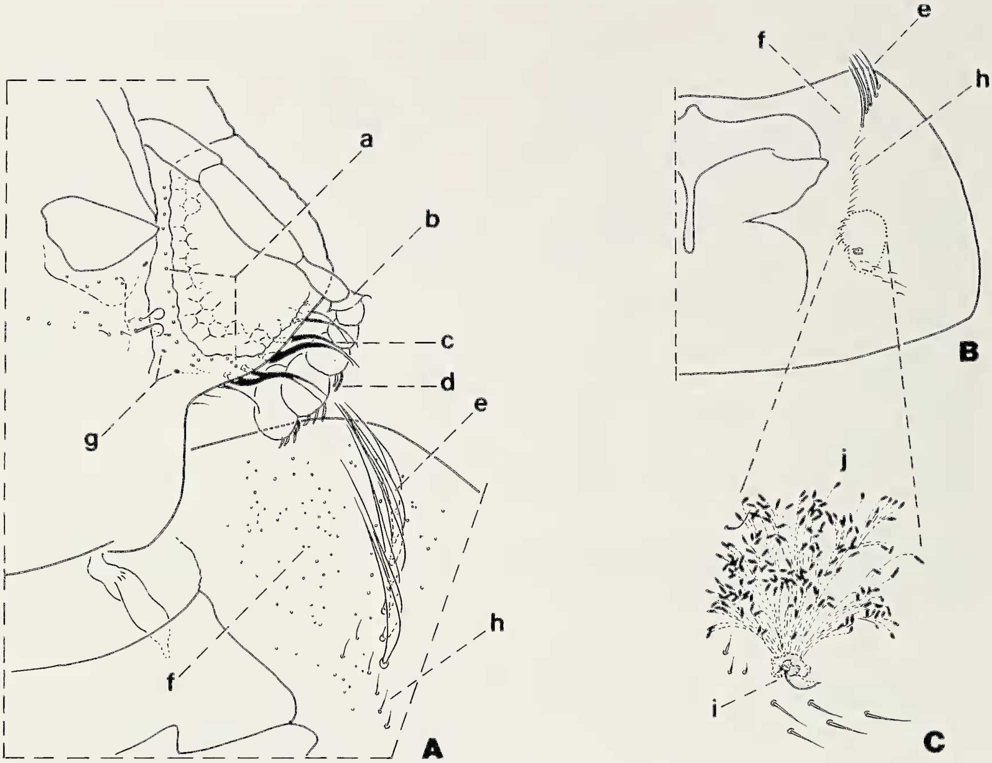


Fig. 26.—*Limnebius truncatellus.* A. Head and adjacent area of prothorax, ventral aspect of left side showing external cuticular features and internal end-apparatus (g) and ductules of exocrine glands. B. Prothorax, ventral aspect of left side. C. End-apparatus and ductules of hypomeral exocrine gland cluster. Structures: (a) periocular exocrine pores, (b) cupule article of antenna, (c) postocular antennal pocket setae, (d) sensilla of antennal club, (e) hypomeral antennal pocket setae, (f) antennal pocket, (g) end-apparatus of exocrine glands, (h) marginal setae of hydrofuge hypomeron, (i) hypomeral glandular fovea, (j) end-apparatus and ductules of hypomeral exocrine gland cluster.

Given these similarities, it seems reasonable to assume that the behavior of *L. piceus* described below is generally representative for the genus. Males of some species of *Limnebius* have highly modified metatibiae. It remains to be determined if this sexual dimorphism relates in some way to secretion-grooming. The metatibiae of *L. piceus* are similar in the sexes.

Secretion-grooming is performed with the beetle "on edge" (Fig. 25A), the legs on one side having the tibiae resting on a wet surface, and the "free" legs on the other side doing the secretion-grooming. Sometimes the beetle (before going on edge) actively moves the mouthparts. Perhaps this behavior serves to spread secretions produced by glands within the mouthparts; it may also serve to remove water by swallowing.

When the beetle is on edge, the prothorax is extended and turned relative to the pterothorax. This positioning of the prothorax "opens" the area around the mesothoracic spiracles, which are located in the intersegmental membrane separating the notal projection of the prothorax and the mesosternum. This position also makes it possible for the legs to contact the posteroventral margin of the

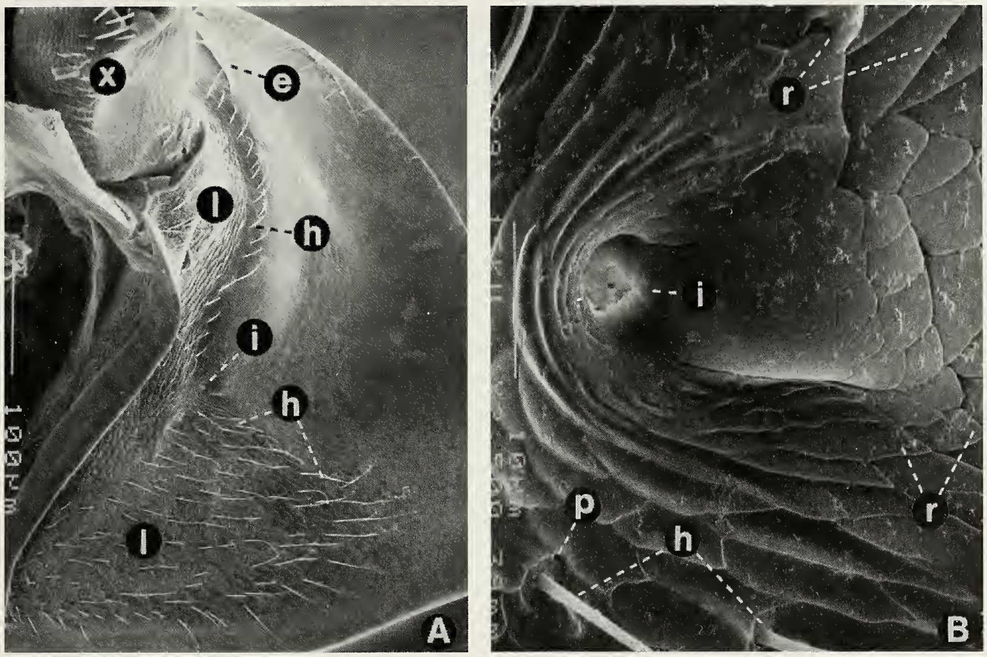


Fig. 27.—*Limnebius truncatellus*. A. Hypomeron, ventral aspect of left side. B. Hypomeral glandular fovea and associated cuticular features. Structures: (e) hypomeral antennal pocket setae, (h) marginal setae of hydrofuge hypomeron, (i) hypomeral glandular fovea, (l) microspiculate hydrofuge, (p) exocrine pore, (r) microreticulation, (x) procoxa.

prothorax and the anterior margin of the elytron, two surfaces which are normally in contact with one another.

The protibia principally rubs four locations: (1) the undersurface of the head, along the antennal groove beneath the eye; (2) the back of the eye, the stroke continuing forward over the top of the eye (Fig. 25B:a); (3) the anterior part of the hypomeron, over the antennal pocket setae (e in Fig. 26A, B and 27A); and (4) over the smooth anterior margin of the elytron (Fig. 25B:b).

Both the profemur and the mesofemur are repeatedly rubbed into the juncture of the prothorax and the mesothorax, and against the area of the hypomeral glandular fovea. Sometimes this rubbing occurs in an alternating pattern, first one leg and then the other. Both the pro- and mesofemur have a distal spine cluster (Fig. 22A, 23A) which contacts the glandular fovea and the surrounding cuticle. The distal spine clusters of both the pro- and mesofemora have some apically flattened and blunt spines, apparently shaped to facilitate spreading the exocrine secretion. In addition to the distal spine cluster, the mesofemur has a unilinear row of spines on the upper surface. These spines are likely involved in rubbing the cuticle during movements in and out of the glandular fovea area.

From time to time the front and middle legs engage in mutual rubbing. This rubbing involves both the femora and tibiae, usually the opposing faces. The anterior face of the mesofemur is provided with short spiniform setae (Fig. 23A) which are involved in the mutual rubbing with the profemur.

The protibial rubbing of the anterior margin of the elytron (mentioned above) occurs as the profemur is rubbed into and out of the exocrine invagination area of the notal projection. The area of the elytron rubbed (Fig. 25B:b) is the extremely smooth anterior margin that the posterior margin of the prothorax slides over when the beetle is in a "normal" body position.

The mesofemur, after being rubbed into the glandular fovea area, is rubbed backwards along the basal part of the elytral epipleuron. In the same motion, the mesotibia rubs the metasternum, stroking backward and outward. Infrequently, the mesotibia is raised over and stroked backward on the lateral upper surface of the elytron (Fig. 25B:c).

The metatibia rubs along the elytral epipleuron. In addition, the metatibia and the metatarsus stroke backward on the upper surface of the elytron (Fig. 25B:d). The tarsus, which is long enough that the tarsal claws reach to the suture between the elytra, rubs a larger surface area than does the metatibia.

One observation was made of partial grooming while the beetle was in the water. First, while obtaining air at the surface of the water, the bubble is made very large by separating the elytra and the abdomen, thereby forming a large bubble under the elytra. After going beneath the water's surface, the elytra and the abdomen are brought back together, forcing the bubble into the prothoracic and head area. In this enlarged bubble the front leg performs grooming movements.

ESDS Cuticular Components.—Like *Hydraena,* the exocrine gland concentration in *Limnebius* is located in the prothorax. However, the organization of the glands with respect to the external cuticular features, and the form of these structures, bear no resemblance to those of *Hydraena.* Although the postocular area has setae that form part of the antennal pocket, these setae appear not to be homologous with the psd-setae of *Ochthebius.*

Hypomeral Glandular Fovea.—The hypomeral glandular fovea is located on the hypomeron, at the margin of the microspiculate hydrofuge (i in Fig. 26B, C and 27). This fovea is supplied by many ductules of the hypomeral exocrine gland cluster (Fig. 26C:j). Cuticular microreticulations (Fig. 27B:r) "fan out" from the glandular fovea such that secretions issuing from the fovea could be spread in both directions, along the lateral margin of the hydrofuge area.

Hypomeral Hydrofuge.—The anterior part of the hydrofuge hypomeron is bordered by a row of marginal setae (Fig. 26:h, 27:h). Similar setae are sparsely distributed over the posterior part of the hydrofuge hypomeron. An exocrine pore is located at the base of some of these setae (Fig. 27B:p).

Antennal Pocket.—The shallow antennal pocket is bordered by a row of about seven closely spaced antennal pocket setae (Fig. 26A:e, 27A:e). No concentration of exocrine gland end-apparatus was found associated with these setae.

Postocular Structures.—The posteroventral margin of the eye is bordered with postocular antennal pocket setae (Fig. 26A:c). Neither a concentration of end-apparatus, nor a secretion sulcus or other kind of secretion reservoir, was found associated with the postocular antennal pocket setae. Only a few singular end-apparatus (Fig. 26A:g) were found. Periocular exocrine pores (FIg. 26A:a) are present.

Femoral Setae.—The stout femoral setae of *L. piceus* (Fig. 22A, 23A, 24A) are in positions consistent with the secretion-grooming behavior. Some setae of the profemoral distal spine cluster are specialized, being flattened and apically blunt, most likely to increase efficiency in spreading secretions of the hypomeral glands.

The details of the distal spine clusters of *Limnebius* differ from those of *Ochth-*

ebius, and the spine clusters rub different body regions in the two genera. This evidence supports the position that the distal spine clusters of *Limnebius* and *Ochthebius* are independently derived.

SYSTEMATICS OF THE FAMILY HYDRAENIDAE

In my monograph of the western hemisphere members of the family (Perkins, 1981), I proposed a very preliminary phylogenetic classification. At that time I suspected that several new genera awaited description, "most likely South African and Australian" (p. 481), and decided to limit the number of genera I treated to 11. The number of genera now known is 37 and, as one would suspect, changes in the proposed phylogeny and classification are required.

More importantly, we now have a much more complete understanding of a critical aspect of the functional morphology of the family; that is, the hypomeral and postocular components of the antennal pocket and the ESDS in its various manifestations.

Hansen (1991) recently reviewed the genera known at that time, proposed groupings of those genera, and discussed several aspects of my proposed (1981) phylogeny and classification. Hansen's (1991) classification and my present classification are comparatively summarized in Figure 71. Hansen's (1991) paper is an excellent catalogue that resolves several nomenclatorial tangles and provides a useful habitus illustration of a representative of almost all genera then known. However, Hansen's (1991) generic (re)descriptions do not present new characters to reveal the relationships of the genera—perhaps a measure of the difficulties posed by this family. The result was, after declaring some of my 1981 groupings as symplesiomorphous, to "force" other genera into those groups.

Some of the characters I used in 1981 have now been superseded by stronger characters, but the higher-level relationships that I tried to emphasis in 1981 remain unchanged: the Ochthebiinae is a separate subfamily, *Limnebius* is more closely related to *Hydraena* than to *Ochthebius,* and the relatively primitive forms I placed in the Hydraenidini are still grouped together, with the exception of *Coelometopon* (moved to a new tribe).

The classification proposed herein is influenced greatly by the new characters of the antennal pocket morphology and the comparative study of the ESDS. The extent to which these new characters have informed the classification will be very apparent from a comparison of the taxonomic key of Hansen (1991) with the keys presented herein.

Although many of the relationships of the genera have been clarified, the relationships among groups at the tribal and subtribal level are still problematic and require the discovery of new character systems. The tribes and subtribes adopted herein emphasize the individuality of the groups, and also reflect the rather high probability that additional new genera, members of the present tribes and subtribes, will be discovered.

Subfamily Ochthebiinae Thomson

Tribe Ochtheosini, **new tribe**

This new tribe is erected for *Ochtheosus,* a new genus known from one fungus-dwelling species from Chile. This genus retains several primitive characters: (1) it is the only known member of the subfamily with 11 antennomeres, the ancestral number for the family; (2) the lacinia and galea, in contrast to all other Ochthebiinae, retain the presumed ancestral condition for the family: brush-like, bearing many slender setae; and (3) the aedeagus has the ancestral condition of fully developed parameres.

In addition to these primitive features, *Ochtheosus* is the only Ochthebiinae to retain the primitive condition for the tentorium. Previously I (Perkins, 1981) suggested that the presence of a "gular sclerite" in the Ochthebiinae was a primitive condition in the family, based on its presence in the outgroups Staphylinidae and Hydrophilidae. However, after studying transparency mounts of representatives of those two families, I conclude that the gular "sclerite" is a secondarily derived feature. In many groups its formation is associated with the posterior elongation of the head to form a "neck." In the Ochthebiini this "sclerite" has resulted from changes associated with the internal strengthening of the anterior part of the tentorium. Therefore, the gular "sclerite" of the Ochthebiini is not homologous with the gular "sclerite" of any other groups, including the Staphylinidae and Hydrophilidae.

The reinforcing of the tentorium, resulting in the formation of an anterior wall with a central "foramen" through which nerves pass (see Perkins, 1981:fig. 151), is absent in *Ochtheosus*. Therefore, the wall structure is a very strong synapomorphic character of the tribe Ochthebiini. This strengthened tentorium is probably structurally related to the other strong synapomorphic character of the Ochthebiini: the lacinia bears enlarged, stout apical teeth.

According to Stickney's (1923) interpretation of the tentorium of Coleoptera, in the ancestral condition the tentorium had, on each side, a small mesial extension termed the laminotentorium. According to this interpretation, ancestrally the laminotentoria were separated one from the other; secondarily, in many unrelated groups, the laminotentoria become fused on the meson.

The hypothetical ancestral (unfused) condition is present in the Orchymontinae and in the Ochtheosini, reflecting the basal origin of these groups. In nearly all Prosthetopinae and (apparently all) Hydraeninae the laminotentoria are fused on the meson, and produced ventrad (in varying degrees; especially developed in some Hydraeninae) as two projections. According to Stickney (1923:39), the condition of fused laminatentoria with ventrad projections is present in many (unrelated) families of beetles. In other words, by this interpretation, the fused condition has independently evolved many times. Rarely in the Prosthetopinae, such as *Prosthetops nitens,* the laminatentoria are not fused; this may be a secondary condition related to the broad head shape.

Ochtheosus, new genus

Type Species.—*Ochtheosus fungicolus,* new species.

Diagnosis.—Recognized among Ochthebiinae by the 11 articles of the antenna, the prominent ocelli located near the midline, the convex and setose dorsum, the ventrally directed maxillary palpi, the shape of the mentum, the small dentiform mesosternal intercoxal process, the large metasternal tabella with median concave impression, the lack of a lateral hyaline border, and features of the antennal pocket.

Description.—**Antennal Pocket**. The subocular antennal groove is smooth, relatively wide, and has very few, ca. six, exocrine pores. The postocular area has a low transgenal ridge demarking the posterior limit of the antennal groove. A very small concavity is present where the transgenal ridge joins the eye margin. No exocrine pores were found associated with the ridge or concavity. The postocular pubescence is well developed and of the reticulate type, whereas the genal pubescence is sparser. Periocular pores were not found on the one specimen studied.

The hypomeral part of the antennal pocket is moderately well developed, its posterior limit well defined by a tranverse ridge. The pocket is microreticulate, except the lateral margin, has numerous exocrine pores, and is nonpubescent except the medial margin. The lateral margin of the pocket forms a strong ridge, but its free edge does not extend to form a hypomeral hyaline border; anteriorly and posteriorly this ridge is contiguous with the corresponding hyaline borders.

The wet-hypomeron is smaller than the bubble-hypomeron, and bears a few strong setae similar to those on the dorsum. A small cluster of short, acute asperites (presumed antennal cleaner) is located on each side of the prosternum, at the margin of the antennal pocket. The profemur has small spines over most of the upper surface; these spines are not organized to form a distal spine cluster such as is present in *Ochthebius*.

Other Characters. Form convex, head deflexed. Dorsum, especially relief of pronotum, strongly setose, each seta with round granule at base. Ocelli prominent, located near midline. Antennomeres 11 (six + club). Maxillary palpi short, arching, with apex directed ventrad; second article slender, slightly arcuate; third article suboval, much wider than other articles; fourth (last) article very slender, slightly shorter than third. Mentum as wide as long. Pronotum with discal relief almost Y-shaped (apical part U-shaped); anterior and posterior hyaline borders narrow, lateral absent. Elytra with even-numbered interseries at least in part with setose granules, sometimes granules joined and elevated to form costae or callosities. Prosternum narrow in front of procoxae, with low midlongitudinal carina. Hypomeron, on ventral face, with well-developed carina forming margin of antennal pocket. Mesosternum with small dentiform process between mesocoxae. Metasternum with large transverse tabella with large median concavity. Intercoxal sternite small, triangular. Legs short, tarsi very short, five–five–five. Hydrofuge pubescence present on postocular area, bubble-hypomeron behind antennal pockets, medial margin of antennal pocket, notal postcoxal projections, mesosternum, metasternum (except tabella), and first and anterior part of second abdominal sterna.

Etymology.—Greek *ochthe* (mountain) plus *eos* (dawn); gender masculine.

Ochtheosus fungicolus, new species
(Fig. 58A)

Type Material.—Holotype male and one paratype of each gender with same data: Chile: Osorno Province, Puyehue Nat. Pk., Anticura, Repucura trail, 500m, bracket and soft fungi, berlese, 19.xii.1984, S. and J. Peck, P#85-41, FMHD#85-926; deposited in FMNH.

Description.—Size (mm × 100; length/width): body 155/80, head 36/54, pronotum 42/69, elytra 110/80. Color dark brown, dorsal setae and ocelli testaceous. Labrum deflexed, wider than long, apical margin with dense fringe of golden setae; apicomedially shining and with small dentiform process in males, shining and simple in females. Frons and clypeus densely granulose and setose. Pronotum more densely setose on reliefs, granulate throughout except shining basal band; lateral margin granulose and setose, sides converging posteriorly. Elytra punctation irregular, especially in distal half and laterally, with "extra" series between costae, noncostate intervals shining. Granulate costae on derivatives of even-numbered intervals as follow: second: present in front of and behind discal saddle; fourth: sinuate, interrupted over short distance near apical third; sixth: complete, sinuate, apically joining costa of fourth; eighth: present over basal half, straight. Elytral margin granulate. Hypomeron with antennal pockets shining, slightly wider than widest part of wet-hypomeron. Metasternal tabella tapering and shining laterally, sparsely pubescent, median fovea slightly wider than mentum, micropunctulate, anterior margin of fovea formed by a thin wall that connects with short apicomedian ridge. Wing reduced to small lobe. Aedeagus (Fig. 58A) with well-developed parameres and short distal process; length 0.36 mm.

Etymology.—Named in reference to the microhabitat.

Discussion.—One additional female specimen of *Ochtheosus* was studied; this specimen differs slightly from the paratype female and may represent a second species: Aisen Province, 33 km E Pto. Aisen, Rio Simpson N. P., 70m, 26.i.1985, forest sifted bracket fungi, S. and J. Peck, P#85-104, FMHD#85-987.

Subtribe Ochthebiina Thomson

This subtribe is erected for the genera *Ochthebius* (type genus), *Gymnochthebius, Hughleechia, Gymnanthelius, Aulacochthebius,* and *Micragasma.* These genera, except perhaps *Micragasma* (see below), have a derived antennal pocket consisting of a postocular area with a secretion distribution sulcus and elongate postocular secretion distribution setae; and a prothorax with a "full complement" of hyaline borders, and comparatively elongate hap-setae.

Hughleechia, judging from its unusual postocular secretion sulcus, probably diverged early in this clade. *Micragasma* Sahlberg is a very rare, monotypic genus from Greece, for which I have had only a few specimens to study. This genus has the full complement of hyaline borders, and a pronotal shape like *Ochthebius* (*Asiobates*). However, based on the few specimens available for study, the postocular area appears to lack both a discrete secretion sulcus and postocular secretion distribution setae. Additional study, with SEM, may reveal that *Micragasma* is another basal group, diverging early in the evolution of the Ochthebiina.

Genus Ochthebius Leach

A determination of the phylogenetic classification of the genus *Ochthebius* has eluded taxonomists from the earliest workers to the most recent. Early workers "split" the genus into many subgenera, later workers "lumped" some and "split" others (see discussion in Perkins, 1981). Recently, several subgenera were synonymized by Hansen (1991) in a review catalogue.

The morphology and behavior elucidated herein provide integrated character systems that clarify the phylogenetic relationships in this group (at least partially; see discussion of *Gymnochthebius*). It is proposed that the genus *Ochthebius* be restricted to species having all the cuticular components of the ESDS, including the (1) postocular secretion delivery (psd-) sulcus, (2) postocular secretion delivery (psd-) setae, (3) hypomeral antennal pocket (hap-) setae, (4) hypomeral hyaline (hh-) border, and (5) lateral hyaline (lh-) border. These species will also have the exocrine glands that empty into the psd-sulcus, the leg-grooming setae, and grooming behavior patterns utilizing these leg setae.

Examples of variations in the ESDS components of *Ochthebius* (as herein defined) are discussed below. Of the species studied, the range of variation in the number of psd-setae is two to eight, with most species having four. The range of variation in the number of hap-setae is three to seven, with most species having either four or five.

Subgenera of *Ochthebius* herein considered valid are thought to be basally derived within *Ochthebius.* Current subgenera are placed into synonymy when found to have ESDS components that are connected by morphocline intermediates to the nominate (and less derived) subgenus (e.g., see *Calobius, Cobalius,* and *Notochthebius* below).

Species with ESDS components that differ from those described above, and appear not to represent systems clearly derived from that of *Ochthebius,* are recognized as distinct genera (e.g., see *Enicocerus* and *Aulacochthebius* below).

Finally, species lacking some (or all) ESDS components (and this absence not appearing to be a result of secondary loss), are recognized at the generic level, separate from *Ochthebius* (e.g., see *Protochthebius* and *Neochthebius* below). Possession of a plesiomorphic condition cannot be used to infer the common ancestry

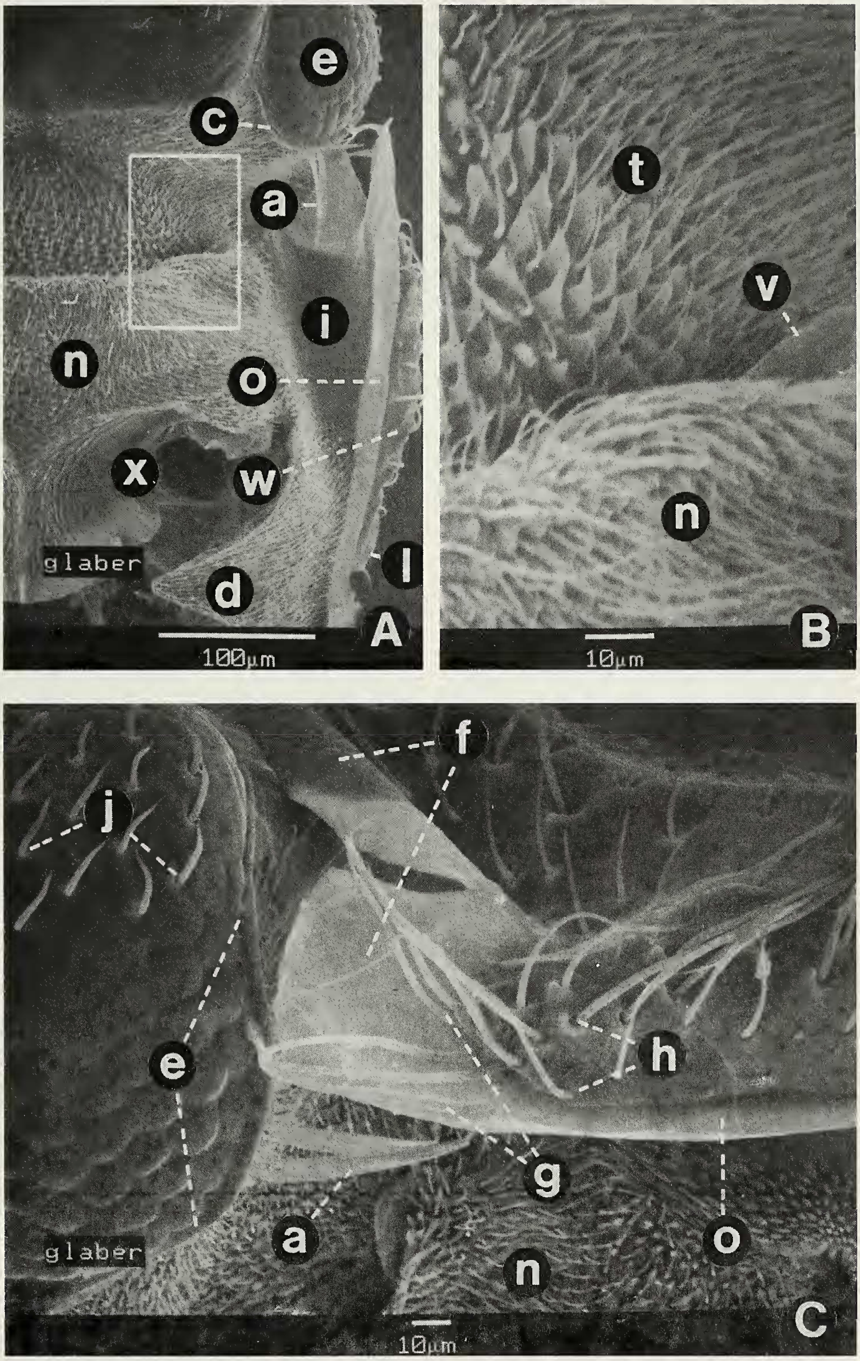


Fig. 28.—*Ochthebius glaber*. A. Venter of left side of head and prothorax. B. Rectangular area of A, enlargement. C. Lateral view of eye and prothorax contact area. Structures: (a) psd-setae, (d) notal postcoxal projection, (e) eye, (f) ah-border, (g) hap-setae, (h) anterolateral pronotal setae, (i) hypomeral antennal pocket, (l) lh-border, (n) prosternum, (o) hh-border, (j) setae of dorsal surface of eye, (t) genal asperite hydrofuge, (v) cervical sclerite, (w) wet-hypomeron, (x) procoxal cavity.

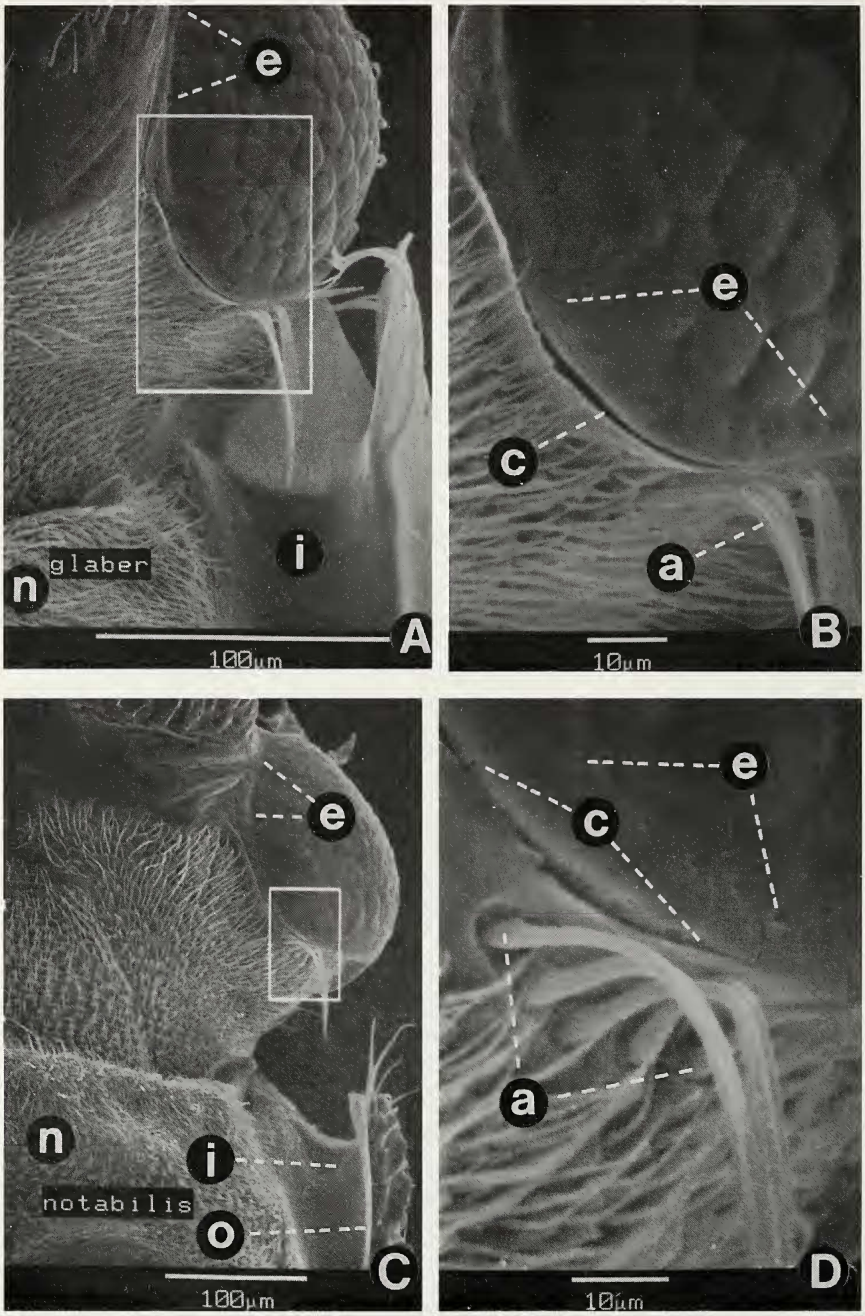


Fig. 29.—*Ochthebius*. A. *O. glaber*, venter of left side of head and prothorax. B. Rectangular area of A, enlarged. C. *O. notabilis*, venter of left side of head and prothorax. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (e) periocular exocrine pores, (i) hypomeral antennal pocket, (n) prosternum, (o) hh-border.

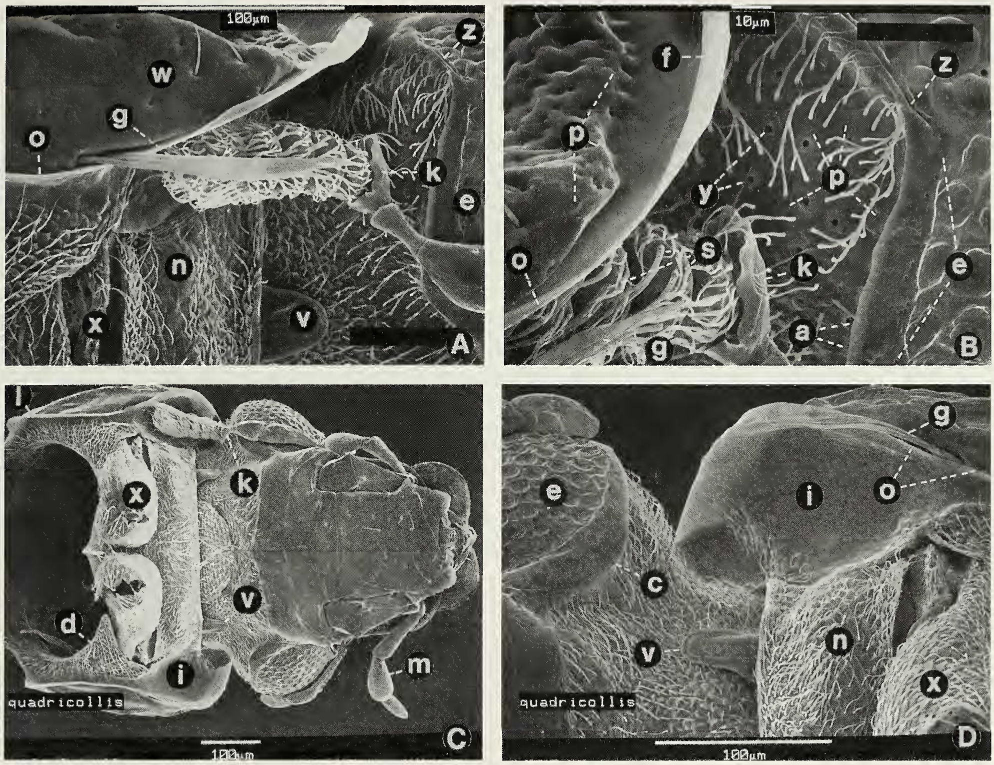


Fig. 30.—*Ochthebius quadricollis,* treated with sodium hydroxide. A, B. Postocular area and adjacent prothoracic structures, right side. C. Venter of head and prothorax. D. Postocular area and adjacent prothoracic structures, left side. Structures: (a) sockets of psd-setae, (c) psd-sulcus, (d) notal postcoxal projection, (e) periocular exocrine pores, (f) ah-border, (g) hap-setae, (i) hypomeral antennal pocket, (k) cupule article of antenna, (l) lh-border, (m) maxillary palpus, (n) prosternum, (o) hh-border, (p) exocrine pores, (s) sensilla of antennal club, (v) cervical sclerite, (w) wet-hypomeron, (x) procoxa, (y) sockets of missing setae, (z) sulcus of (?)periocular pores.

of species with that condition. Therefore, detailed study should be given forms that lack ESDS components.

Subgenera *Calobius* Wollaston and *Cobalius* Rey, **new synonymy**

The effectiveness of the ESDS in revealing phylogenetic relationships, and mistaken methods, is well demonstrated by the so-called subgenera *Calobius* and *Cobalius.* The ESDS components of *Calobius,* represented by *Ochthebius quadricollis,* differ from *Ochthebius* (sensu stricto) in three major respects (the type species, *Calobius heeri* Wollaston, is a junior synonym of *O. quadricollis*). All of these features, relative to the ESDS of *Ochthebius* (sensu stricto), must be considered *derived* conditions.

The ESDS components of *O. quadricollis* (Fig. 2B; 30; 33A, B) are as follow: (1) the psd-sulcus (Fig. 33B:c) is smaller, the postocular pores at the sulcus being concentrated in a smaller area; in whole mounts, this area appears distinctively more heavily sclerotized and more complex than the same area in *Ochthebius* (sensu stricto); (2) the hap-setae (Fig. 2B:g) arise more posteriorly, opposite the trochanter; however, these hap-setae are very long and their tips attain a position—

contacting the psd-setae—similar to that attained by their homologues in *Ochthebius* (sensu stricto); and (3) the hh-border is not as wide as is generally found in *Ochthebius* (sensu stricto) (Fig. 30:o).

The two "subgenera," *Calobius* and *Cobalius,* were recently revised by Jäch (1989, 1993), who considered them distinct and unrelated. Jäch (1993:33) states, "*Calobius* is obviously not very closely related to any other genus or subgenus of the subfamily Ochthebiinae," and ". . .a generic status for *Calobius* could be taken into consideration." Regarding *Cobalius,* Jäch (1989:41) remarked that "It differs from all other subgenera of *Ochthebius* by the peculiar dentation of the elytral margin."

In his revision of *Cobalius,* Jäch (1989) described a new species, *Ochthebius* (*Cobalius*) *celatus.* Thorough study of this species, however, reveals that the ESDS is virtually identical to that of *O.* (*Calobius*) *quadricollis.* This evidence, which is supported by the overall external resemblance of these two species (except the denticulate margin of *O. celatus,* see below), clearly indicates that these two species are very closely related.

Jäch (1992*a*:7) used "a very large head" to characterize *Calobius,* and in 1993 (p. 33) stated that "*Calobius* is easily distinguished from other subgenera of *Ochthebius* by the wide head and pronotum, by the strongly reduced epipleura, which are ended before the middle of the elytra and by the missing explanate margin of the elytra. . . ."

However, measurements of *O. quadricollis* show that the length/width proportions of the head and pronotum each differ insignificantly, or not at all, from the proportions found in other *Ochthebius* (sensu stricto). This is also true of the proportions of the elytra. In other words, neither the head nor the pronotum is wide. Rather, it is the pterothorax (and elytra) that are derived, via size reduction, consistent with the reduced condition of the elytral epipleura and loss of the explanate elytral margin.

Ochthebius serratus Rosenhauer and *Ochthebius adriaticus* Reitter, two other species that Jäch (1989) placed in *Cobalius* (based on the superficial character of denticulate elytral margins), are, in fact, with respect to the placement of the hypomeral antennal pocket setae, morphocline intermediates between *Ochthebius* (sensu stricto) and "*Calobius*" *quadricollis.*

The morphocline of hap-setae number and placement in this clade is as follows. In the ancestral condition, the hap-setae are closely clustered at the anterior angle of the hypomeron (opposite the anterior margin of the prosternum) and usually four or five in number (e.g., *O. marinus*; Fig. 31A). In *O. serratus* the hap-setae are five in number, and in a line, with the socket of the most posterior seta of the row being opposite, or nearly so, the midlength of the prosternum (Fig. 31B). In *O. adriaticus* and *O. subinteger* the hap-setae are reduced to four, and are located more posteriorly, opposite the trochanter of the front leg (Fig. 31C, D). Finally, in *O. quadricollis, O. celatus,* and *O. lejolisi* (the type species of *Cobalius*) the hap-setae are reduced to three in number, and these are positioned opposite the trochanter (Fig. 2B; 30A; 31E, F).

The polarity of this morphocline is not based primarily on an outgroup comparison. It simply makes more sense for the hap-setae to have initially evolved where they would be of use, despite their comparatively small size. This location is at the anterior extreme of the hypomeron, where the tips of the setae (even when quite small) could "bridge the gap" at the marginal area of the bubble, between the antennal pocket and the postocular area of the head. This ESDS

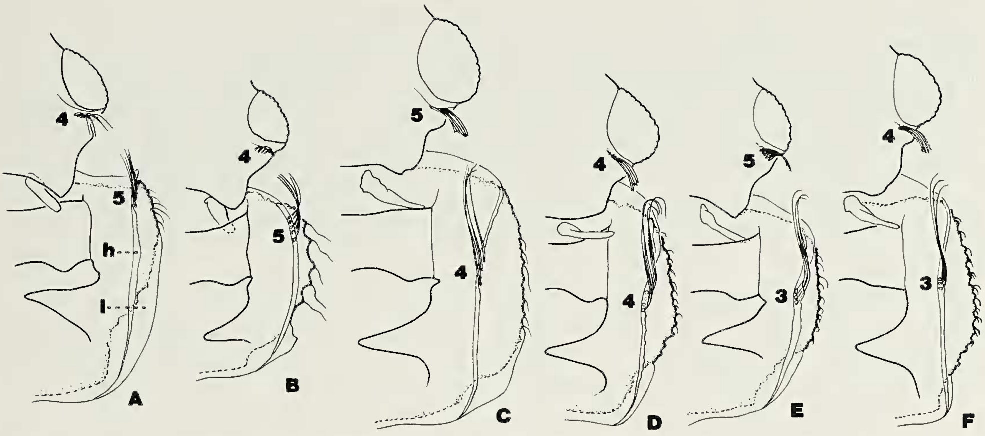


Fig. 31.—*Ochthebius* spp., ventral aspect of head and prothorax, left side, illustrating ancestral condition (A) and morphocline of hap-setae of *quadricollis* group species. Numbers of psd-setae and hap-setae indicated. A. *O. marinus*, hh-border (h) and lh-border (l). B. *O. serratus*. C. *O. adriaticus*. D. *O. subinteger*. E. *O. celatus*. F. *O. lejolisi*.

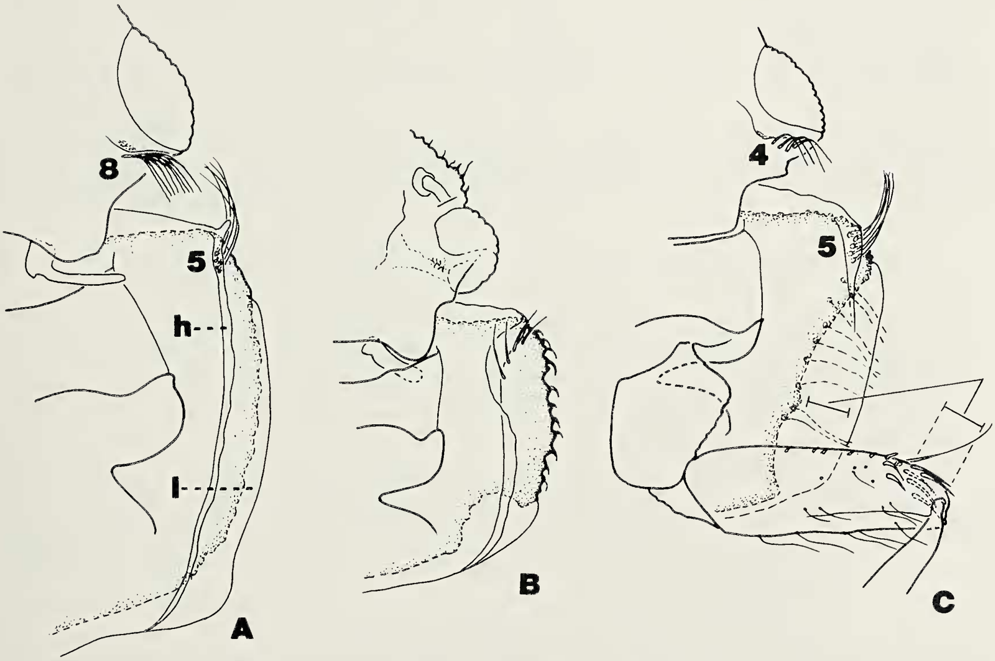


Fig. 32.—Ventral aspect of head and prothorax, left side. Numbers of psd-setae and hap-setae indicated. A. *Ochthebius capensis*, hh-border (h) and lh-border (l). B. *Micragasma paradoxum*. C. *Ochthebius spatulus*, illustrating the loss of posterior part of the hh-border, and the correlation of width of the lh-border and length of setae in the profemoral distal spine cluster.

component morphocline clearly reveals that *Calobius* is a comparatively recent derivative within the species group *Calobius* + *Cobalius*.

The elytral and pronotal denticles present in *O. celatus* Jäch and, for example, "*Cobalius*" *serratus* Rosenhauer, could, of course, be interpreted as being independently derived. However, given the morphocline relationship of the ESDS of *serratus–celatus–quadricollis,* a more likely morphological history is that the denticulate margins were inherited from the common ancestor of *Calobius* + *Cobalius.* Of course it is difficult to have appropriately shaped margins when margins do not exist.

The dorsum of *O. serratus* has the presumed ancestral condition of comparatively rough sculpture, the pronotum being foveate, and the marginal denticles comparatively prominent. In *O. celatus* the dorsum is much smoother, the pronotum virtually nonfoveate, and the denticles smaller. In *O. quadricollis* the denticles (together with the explanate margin) are lost without a trace.

Correct species-group placement of all of the other species included in Jäch's 1989 revision of "*Cobalius*" requires an examination of the ESDS components of each species. *Ochthebius subinteger* Mulsant and Rey is a member of this group. In the one specimen of this species I was able to study, the left side had four hap-setae, and the right side had three hap-setae (positioned as in *O. quadricollis* and *lejolisi*). At least two species of this group, *O. adriaticus* and *O. subinteger,* have a derived condition of the psd-setae: the setae are flattened and the apices are blunt and jagged (Fig. 31C, D).

I hereby synonymize both *Calobius* Wollaston and *Cobalius* Rey with *Ochthebius* Leach. The literature citations and type species are given by Hansen (1991) and need not be repeated here.

All members of this clade, which is properly referred to as the *quadricollis* species group, are apparently halophilic. Some members of the group, for example *O. quadricollis,* have secondarily developed a more brush-like condition of the lacinia and galea—perhaps reflecting a difference between the microfaunal food sources present in marine rockpools and those present in freshwater microhabitats.

Subgenus *Liochthebius* J. Sahlberg, **new synonymy**

This monotypic subgenus was established for *Ochthebius eburneus* J. Sahlberg, a species from Tunis. Although this species is unusually smooth dorsally, and has an unusually spinose labrum, the pronotal shape is typical of *Ochthebius* (sensu stricto), and the ESDS is clearly a slightly derived variety of the *Ochthebius* (sensu stricto) configuration.

The antennal pocket is relatively wide and smooth, and the wet-hypomeron is, correspondingly, quite narrow. The hypomeral hyaline border, at its posterior extreme, merges with the anterior extreme of the quite narrow lateral hyaline border. There are three psd-setae, apically pointed and of usual length. There are three hap-setae, originating from the anterior extreme of the wet-hypomeron; these setae are slightly longer than usual for the genus (only one specimen, from the type series, was studied). The ESDS components and the dorsal habitus leave no doubt that *O. eburneus* is simply yet another slightly specialized form within *Ochthebius* (sensu stricto). I hereby synonymize *Liochthebius* J. Sahlberg with *Ochthebius* Leach. Refer to Hansen (1991) for literature citations and type species.

Subgenus *Notochthebius* Orchymont, **new synonymy**

The subgenus *Notochthebius* was described by Orchymont for the single South African species *Ochthebius capicola* (Péringuey). The ESDS of *O. capicola* has all of the derived features present in *Ochthebius* (sensu stricto). All hyaline borders are present, and the hap-setae are five in number and clustered near the anterior angle of the hypomeron.

The ESDS of *O. capicola* differs from *Ochthebius* (sensu stricto) in having the derived condition of eight psd-setae (Fig. 32A), and in having the psd-sulcus shorter (like *O. rubripes*; Fig. 34D), with the exocrine pores more concentrated and the internal part of the reservoir more heavily sclerotized (i.e., internally more complex than in *Ochthebius* [sensu stricto]). *Ochthebius capicola* has no characters from which can be inferred a basal origin within *Ochthebius*. *Notochthebius* Orchymont is hereby placed in synonymy with *Ochthebius* Leach. Refer to Hansen (1991) for literature citations and type species.

Subgenus *Nyxochthebius* Orchymont, **new synonymy**

The subgenus *Nyxochthebius* was described by Orchymont for the single Namibian species *Ochthebius rubripes* Boheman. Recently, Perkins and Balfour-Browne (1994) compared some aspects of the dorsal and abdominal morphology of *O. rubripes* and *O. capicola,* and considered *Nyxochthebius* a junior synonym of *Notochthebius*.

The ESDS of *O. rubripes* entirely confirms this relationship and synonymy: the ESDS parts are virtually identical to those of *O. capicola,* including the derived condition of the psd-sulcus (internally complex) and psd-setae (eight in number; Fig. 9; 33C, D). *Nyxochthebius* Orchymont, 1933, is hereby "formally" synonymized with *Ochthebius* Leach, 1815. Refer to Hansen (1991) for literature citations and type species.

Ochthebius (sensu stricto) *capicola* and *O.* (sensu stricto) *rubripes,* the two species comprising the *capicola* group, are found in marine rockpools, as are most (if not all) species in the *quadricollis* group. The evolutionary process of loss of dorsal sculpture has independently occurred in the two groups. As noted above, in the *quadricollis* group the rough ancestral sculpture has been retained by *O. serratus*. In the *capicola* group it is *O. rubripes* that retains the more roughly sculptured dorsum (see also Perkins and Balfour-Browne, 1994).

The internally more complex psd-sulcus of members of the *capicola* group and some members of the *quadricollis* group, together with the unusual habitat of these species, suggests that perhaps species in this microhabitat are experiencing selection for more copious production of the exocrine secretions. This is also suggested by the large number (eight) of psd-setae present in *O. capicola* and *O. rubripes*. The selective elements may be the salinity of the water, the turbulence of the rockpools, or perhaps the kinds of "ESDS fouling" microorganisms present in these rockpools.

Subgenus *Asiobates* Thomson
(Fig. 1D, 35)

The ESDS of the subgenus *Asiobates* is very similar to that of *Ochthebius* (sensu stricto). In some species, for example *O. angularidus* (Fig. 1D), the periocular pores are quite large and well separated from the postocular pores. Addi-

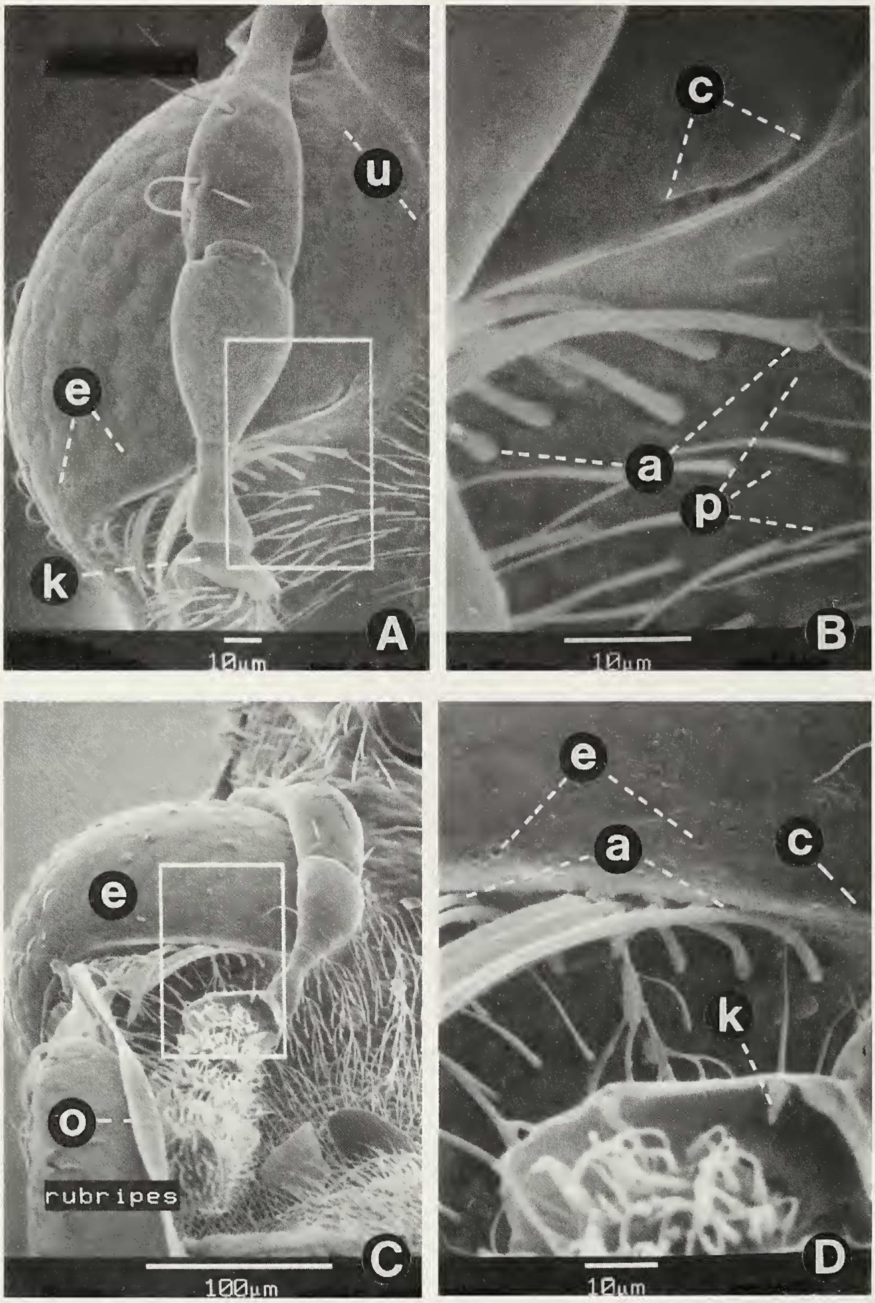


Fig. 33.—*Ochthebius*, venter of eye and adjacent structures. A. *O. quadricollis*. B. Rectangular area of A, enlarged. C. *O. rubripes*. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (e) periocular exocrine pores, (k) cupule article of antenna, (o) hh-border, (p) exocrine pores, (u) subocular antennal groove.

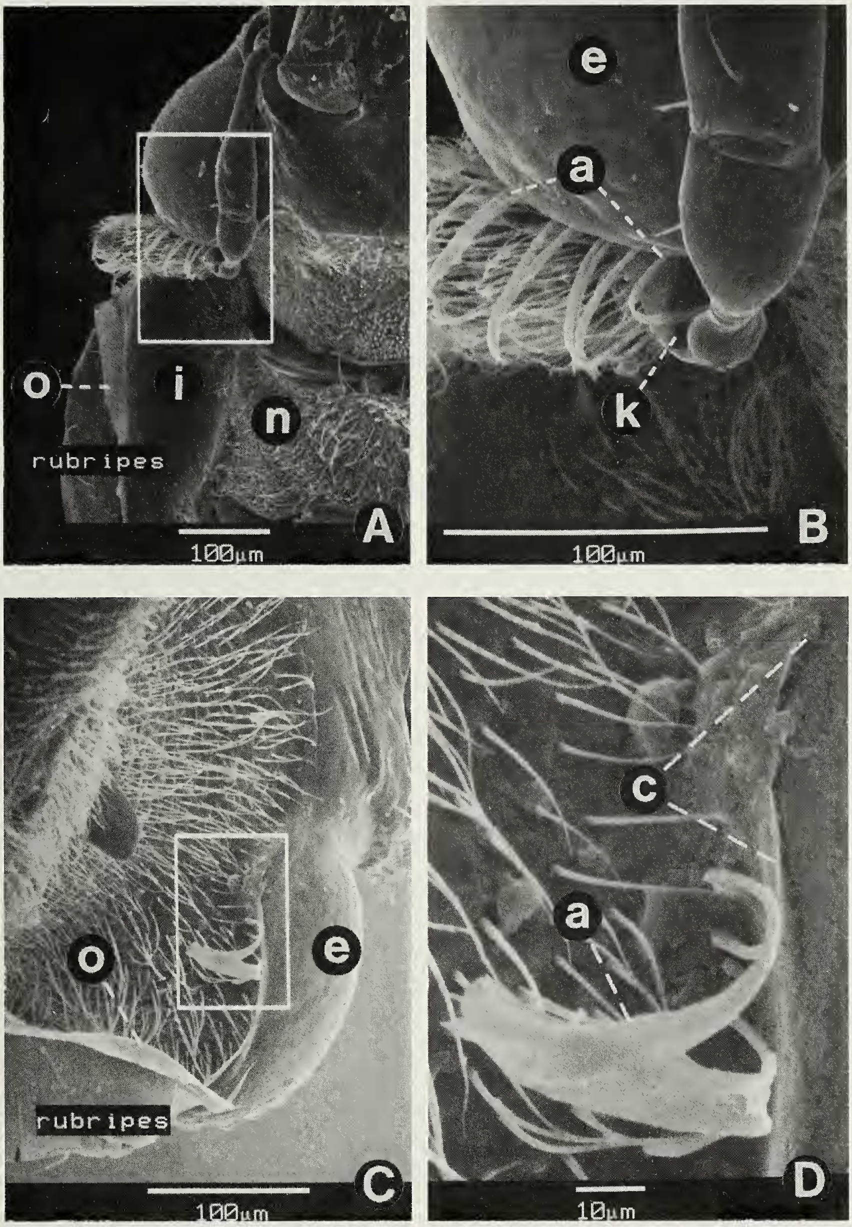


Fig. 34.—*Ochthebius rubripes.* A. Ventral aspect of head and prothorax. B. Rectangular area of A, enlarged. C. Posterior aspect of subocular area. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (d) end-apparatus and ductules of exocrine glands, (e) eye, (i) hypomeral antennal pocket, (k) cupule article of antenna, (n) prosternum, (o) hh-border.

tionally, often the psd-setae are oriented slightly differently than those of *Ochthebius* (sensu stricto), being less sinuate at their bases (Fig. 1D:a, 35B:a).

The psd-setae vary in number from two or three (see *bicolon,* below) to five or perhaps six (in the species studied), with a tendency toward having the posterior

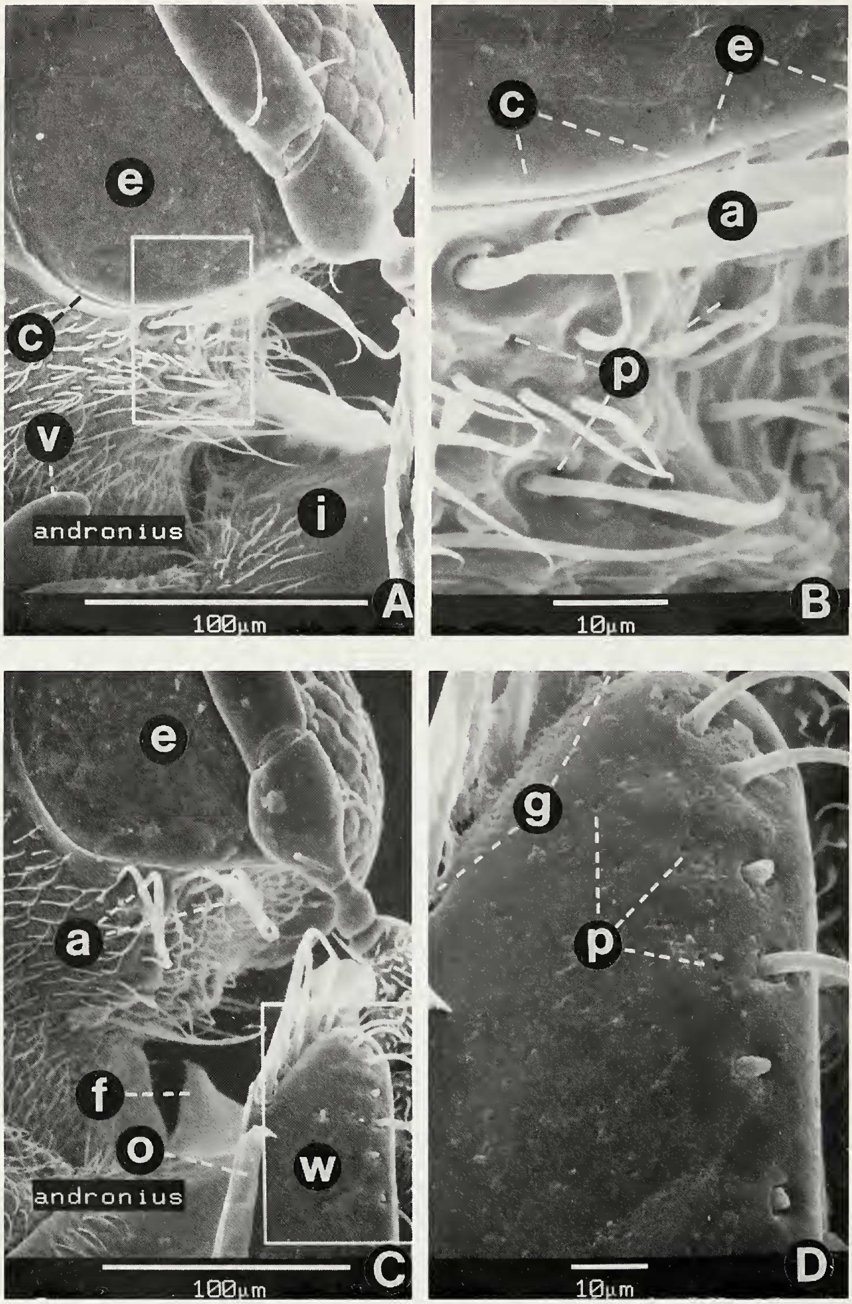


Fig. 35.—*Ochthebius andonius.* A. Venter of eye and adjacent prothorax. B. Rectangular area of B, enlarged. C. Venter of eye and adjacent prothorax. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (d) end-apparatus and ductules of exocrine glands, (e) eye and periocular exocrine pores, (f) ah-border, (g) hap-setae, (i) hypomeral antennal pocket, (o) hh-border, (p) exocrine pore clusters of wet-hypomeron, (v) cervical sclerite.

two or three setae much larger than the anterior setae. The setae are always located at or near the anterior extreme of the hypomeron. The shapes vary, including flattened or nonflattened, the tips pointed, sometimes abruptly so, sometimes elongate and very gradually tapering to form slender tips.

Preliminary comparisons indicate that there is at least some consistency in the number and shape of the psd-setae—at the species-group level—that may be useful for diagnosing members of species clusters that have a more derived condition (e.g., few or many psd-setae, elongate tips, and size differences among the setae).

In *O. bicolon* Germar (the type species of *Asiobates, O. rufomarginatus* Erichson, is a junior synonym), there are only two psd-setae (some variation in number might be expected); these setae taper gradually and are not flattened. There are four or five hap-setae, the two most posteriorly placed being much larger than the others. The hh-border is wide at the hap-setae, the latter not extending greatly beyond the hyaline border.

Contrastingly, in *O. angularidus* Perkins there are four psd-setae, less tapering than those of *O. bicolon.* There are five hap-setae, all about equal in length, closely and regularly spaced (in a row), and each extending well beyond the free margin of the hh-border.

Asiobates is retained as a valid subgenus for the following reasons: (1) the monophyly of the group is strongly suggested by the consistent shape of the aedeagus, with the parameres diverging from the main-piece (Perkins, 1981:295); (2) the characteristic pronotal shape, with the posterior sides sharply "excavate"; (3) despite the high morphological diversity and wide geographical range of both *Asiobates* and *Ochthebius* (sensu stricto), there are no known transitional morphocline intermediates (in 1 and 2 above) between them; and (4) there is some evidence suggesting that *Asiobates* diverged basally in *Ochthebius* (see *Micragasma,* below).

The placement of *Homalochthebius* as a synonym of *Asiobates* by Perkins (1981) is corroborated by the ESDS. For example, a species formerly placed in *Homalochthebius, O. andronius* Orchymont (Fig. 35) is similar to other *Asiobates* in features of the ESDS, except that there are more psd-setae (five) and more hap-setae (six to eight) than the number present in most species of *Asiobates* (four and four to six, respectively). In other words, the ESDS of members of the "*Homalochthebius*" group represents a derived condition within *Asiobates.*

Genus *Gymnochthebius* Orchymont
(Fig. 36, 51C)

Members of *Gymnochthebius* that I have been able to study were found to have a postocular and hypomeral antennal pocket structure very similar to that of *Ochthebius.* For example, in *Gymnochthebius plesiotypus* (Fig. 36) the postocular area has a well-developed secretion sulcus (Fig. 36:c) and secretion delivery setae (Fig. 36:a), and the hypomeral antennal pocket has a hyaline border (Fig. 36:o) and hap-setae (Fig. 36:g) opposite the psd-setae.

However, there are many differences between the two groups, including aedeagal and spermathecal structure (see Perkins, 1981), abdominal vestiture (see *Aulacochthebius,* below), leg structure, and greater development of hypomeral glands in *Gymnochthebius* (described below). The aedeagal and abdominal structures of *Gymnochthebius* suggest a closer relationship to *Aulacochthebius* and

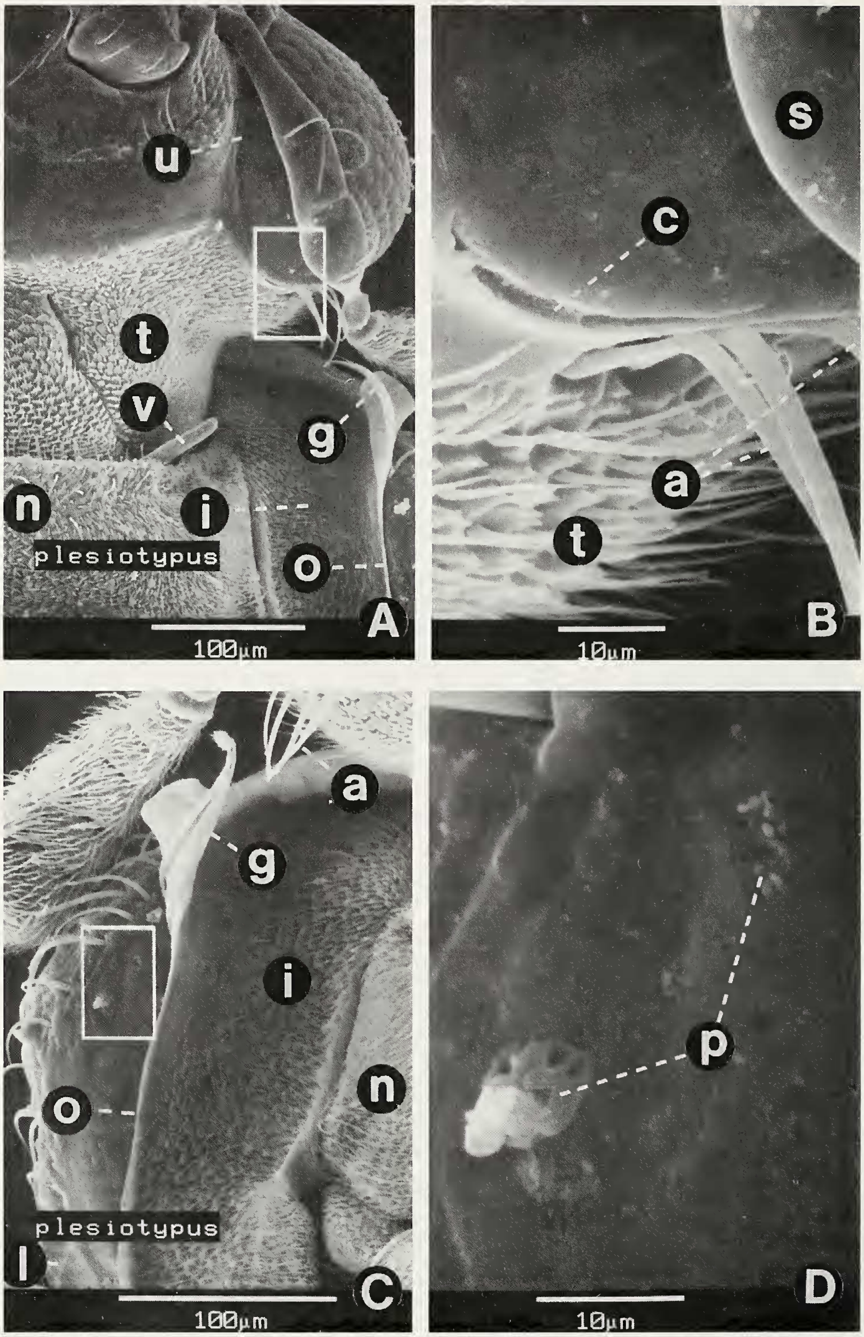


Fig. 36.—*Gymnochthebius plesiotypus.* A. Venter of head and prothorax. B. Rectangular area of A, enlarged. C. Antennal pocket area of prothorax. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (g) hap-setae, (i) hypomeral antennal pocket, (l) lh-border, (n) prosternum, (o) hh-border, (p) exocrine pore clusters, with secretion, (s) second antennomere, (t) genal and post-ocular asperite hydrofuge, (u) subocular antennal groove, (v) cervical sclerite.

Gymnanthelius than to *Ochthebius*. These similarities and differences suggest that *Gymnochthebius* diverged basally within the Ochthebiina. Study of additional species are necessary to discover the full range of variation in the ESDS of *Gymnochthebius*.

The hypomeral exocrine glands of *Gymnochthebius plesiotypus* (Fig. 51C) comprise two types, based on shape of the end-apparatus: (1) spermoid—sperm-shaped (similar to those in Fig. 3), with long ductules relative to the size of the end-apparatus (Fig. 3:b). The pores (Fig. 51C:a) for these glands are solitary, and are present principally in the nonhydrofuge pubescent part of the antennal pocket; and (2) tubuloid—tubule-shaped, with short ductules relative to the length of the end-apparatus. On the wet-hypomeron the pores of these glands are grouped into four distinct clusters, each with about seven pores (Fig. 36C, D; 51C:c, t). Additional tubuloid glands are found singly along the posterior part of the hypomeron.

Genus *Aulacochthebius* Kuwert, **new status**
(Fig. 37)

In *Aulacochthebius* a postocular secretion sulcus (Fig. 37:c) is present. The ridge of the sulcus is continuous with a transgenal ridge (Fig. 37:z); this carina is absent in *Ochthebius*. The psd-setae (Fig. 37:a) are relatively short, slightly widened from base to apex, flattened, and apically fringed. Periocular pores (Fig. 37:e) are present.

The hypomeral antennal pocket (Fig. 37:i) is well developed, smooth, and nonpubescent, except hydrofuge pubescent anteromedially. The hh-border is well developed, contiguous anteriorly with the ah-border, posteriorly passing across the ventral surface of the well-developed lh-border, and contiguous with the ph-border. The hypomeral antennal pocket setae (Fig. 37:g) are well developed, flattened, about five in number, and about twice as long as the hh-border is wide. The wet-hypomeron is well developed. The profemur has a well-defined distal spine cluster, the spines few in number but distinctly larger than other profemoral spines.

This genus is currently being revised by the author. *Aulacochthebius* appears to be most closely related to *Gymnochthebius*, based on the aedeagal and abdominal structures. In contrast to *Ochthebius*, both genera have the abdominal sterna clothed in a combination of hydrofuge setae and stiff, erect spines.

Gymnanthelius, **new genus**
(Fig. 38, 39)

In *Gymnanthelius hieroglyphicus* (Deane), the type species of the genus *Gymnanthelius*, a specialized ESDS is present, but the components differ in several respects from those of *Ochthebius*. The postocular area near the posteroventral angle of the eye has a strongly microreticulate shelf that terminates in a spiculate secretion area (Fig. 38:z, 39:z), with exocrine pores. This spiculate margin is continuous with a transgenal ridge (Fig. 39:r). Adjacent to the spiculate secretion area are three specialized plumose secretion delivery setae (Fig. 38:a, 39:a), each with multiply-branched tips.

The genal hydrofuge (Fig. 38:t, 39:t) is strongly asperite, but the postocular area near the delivery setae is rather sparsely pubescent and smooth. Periocular pores (Fig. 38:e, 39:e) are present adjacent to the eye facets. The hypomeral antennal pocket (Fig. 38:i, 39:i) is well developed, smooth except for an antero-

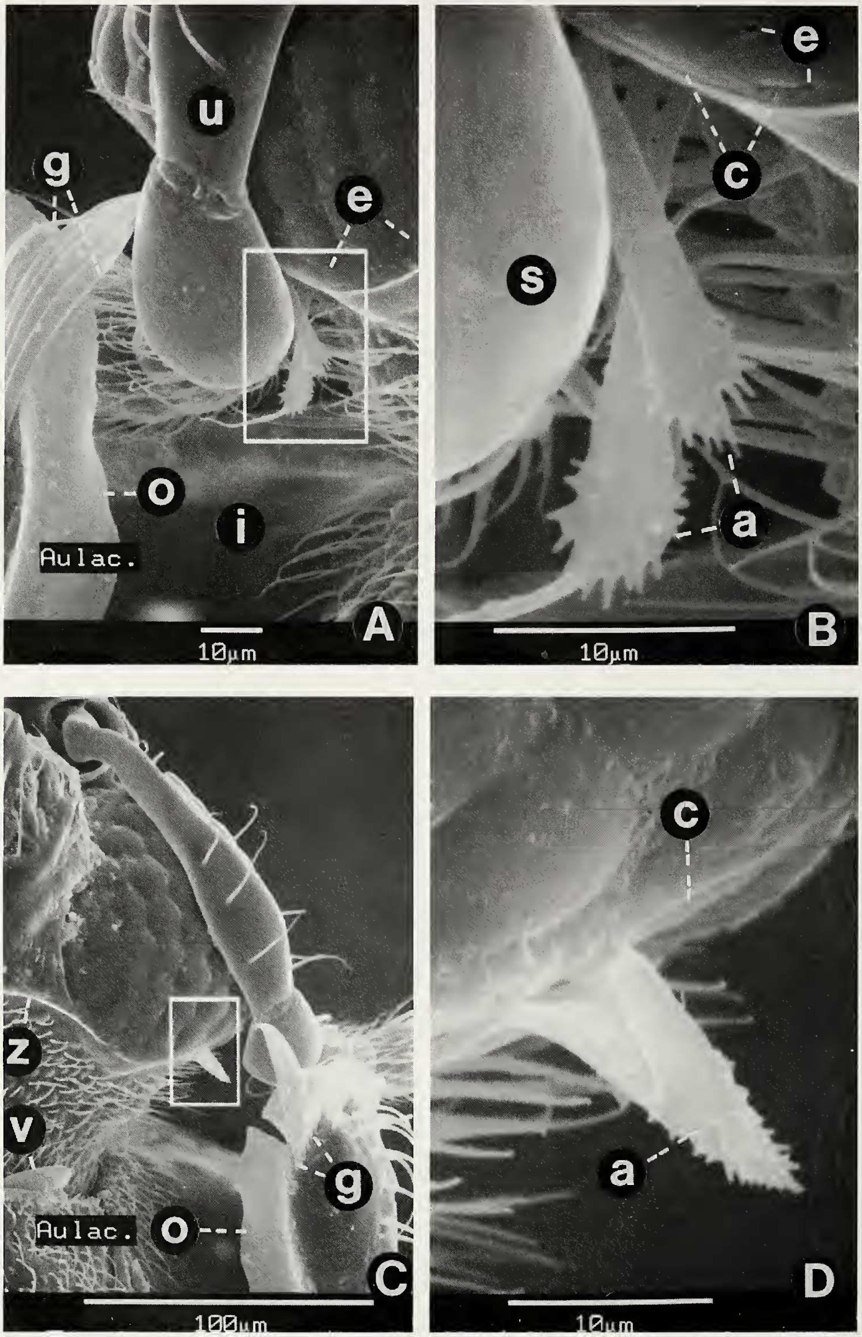


Fig. 37.—*Aulacochthebius* sp. A. Postocular and adjacent hypomeral areas. B. Rectangular area of A, enlarged. C. Venter of head and adjacent prothorax. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (e) periocular exocrine pores, (g) hap-setae, (i) hypomeral antennal pocket, (o) hh-border, (s) second antennomere, (u) first antennomere, (v) cervical sclerite, (z) transgenal ridge.

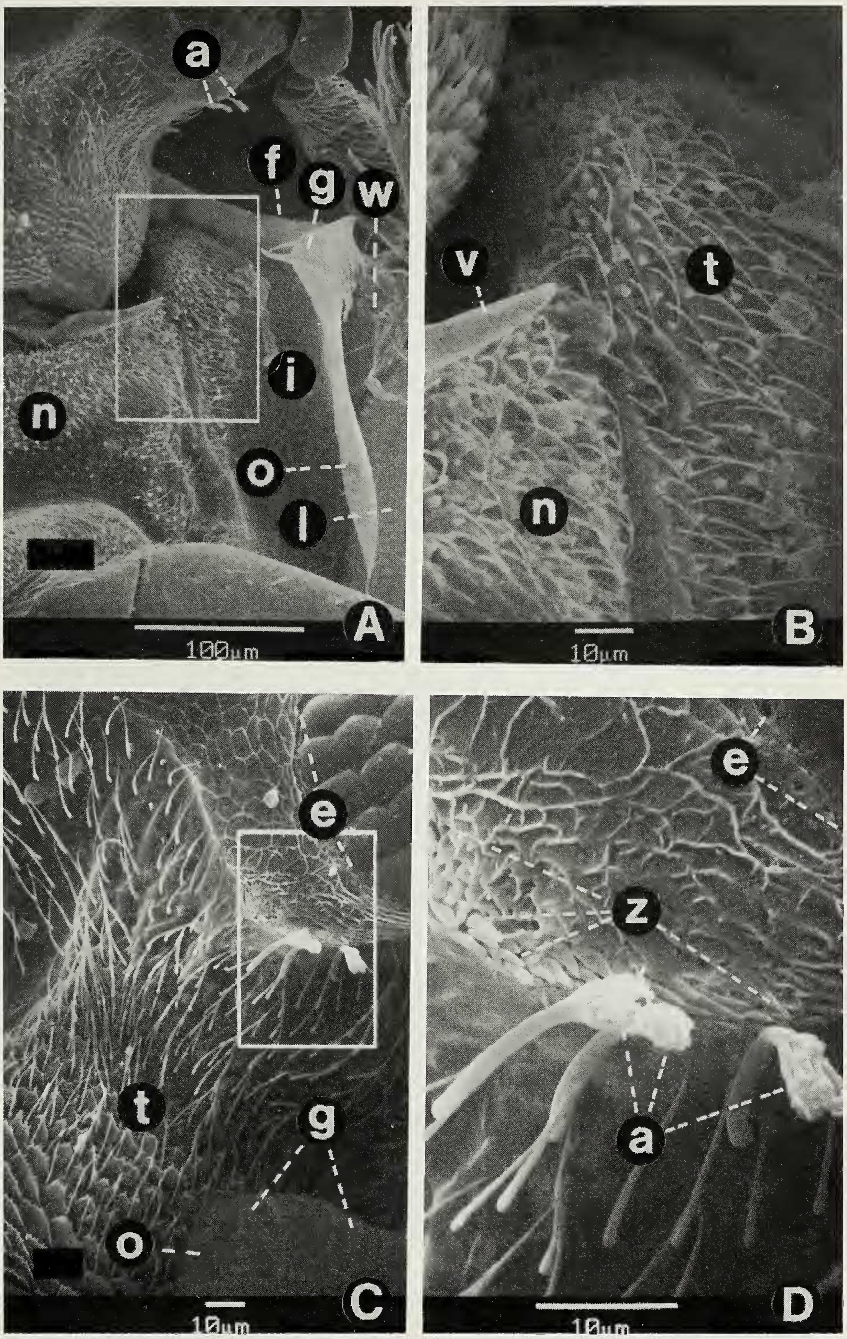


Fig. 38.—*Gymnanthelius hieroglyphicus*. A. Venter of head and prothorax, left side. B. Rectangular area of A, enlarged. C. Postocular area, posteroventral aspect. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (e) periocular exocrine pores, (f) ah-border, (g) hap-setae, (i) hypomeral antennal pocket, (l) lh-border, (n) prosternum, (o) hh-border, (t) asperite hydrofuge, (v) cervical sclerite, (w) wet-hypomeron, (z) postocular exocrine secretion distribution area.

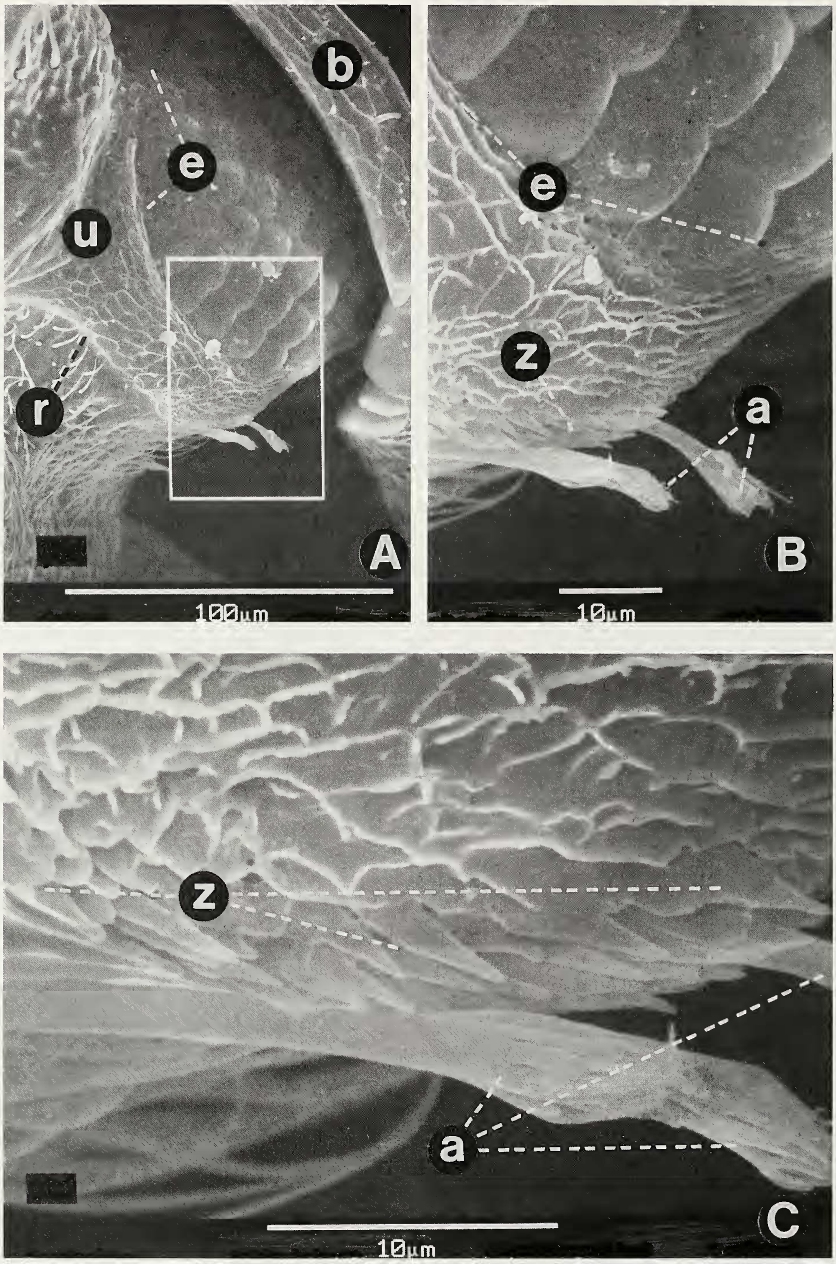


Fig. 39.—*Gymnanthelius hieroglyphicus.* A. Venter of left eye. B. Rectangular area of A, enlarged. C. Postocular exocrine secretion distribution area. Structures: (a) psd-setae, (b) first antennomere, (e) periocular exocrine pores, (r) transgenal ridge, (u) subocular antennal groove, (z) postocular exocrine secretion distribution area.

medial asperite hydrofuge area (Fig. 38:t). The hypomeral, lateral, anterior, and posterior hyaline borders are all well developed. The hypomeral antennal pocket setae (Fig. 38:g) are short (relative to those of *Ochthebius*), extending only slightly beyond the hh-border. The wet-hypomeron (Fig. 38:w) is small. The profemur has a distal cluster of strong spines.

The structures of the postocular area, especially the spiculate exocrine area, do not seem to be a condition derived from the secretion sulcus of *Ochthebius*. It is problematic whether or not the secretion delivery setae of *Gymnanthelius* are homologous with those of *Ochthebius*. A more complete description of this new genus, together with descriptions of additional species, will be presented elsewhere.

Genus *Hughleechia* Perkins
(Fig. 40)

The genus *Hughleechia* is based on *H. giulianii* Perkins, an intertidal species from Australia (Perkins, 1981). The second known species of *Hughleechia*, an undescribed intertidal species from Tasmania, is similar to *giulianii* in structures of the ESDS, but quite dissimilar to that species in several other external features.

Unlike *Ochthebius*, the postocular area does not have a secretion sulcus near the posteroventral angle of the eye. There is, however, a transgenal secretion sulcus (Fig. 40:z). The cuticle is distinctively raised on each side of the sulcus to form a transgenal ridge. The secretion delivery setae (Fig. 40:a) are elongate and appear to be paired. The postocular hydrofuge (Fig. 40:t) is asperite and has exocrine pores (Fig. 40:p) near the base of the secretion delivery setae.

The hypomeral antennal pocket (Fig. 40:i) is well developed, the cuticle smooth except microreticulate medially and hydrofuge pubescent anteromedially. Exocrine pores are moderately dense in the antennal pocket. The hh-border (Fig. 40:o) is quite large anteriorly, such that it contacts the psd-setae. In its posterior part, the hh-border is quite narrow and becomes contiguous with the ph-border. The posterior border of the pronotum is arcuate such that there are no posterior angles. In *H. giulianii*, the hh-border and ah-border are not contiguous, the ah-border being absent over the area of the postocular emarginations of the pronotum (Fig. 40A). In the undescribed species, however, the two hyaline borders are contiguous. The wet-hypomeron is well developed. The lh-border is absent. The hypomeral antennal pocket setae are present, but unlike *Ochthebius*, do not extend beyond the hh-border. The profemur does not have a distal spine cluster, the spines in this area being small as are others on the profemur.

Subtribe Meropathina, **new subtribe**

This new subtribe comprises the genera *Meropathus* (type genus), *Tympallopatrum*, and *Tympanogaster*. Members of the subtribe have a primitive antennal pocket. The metasternum has a large glabrous area or tabella (a derived condition), except in *Meropathus* where the metasternum is greatly reduced—associated with flightlessness. All known members are south temperate (Gondwanan) in distribution.

These genera form a distinct clade based on the derived condition of the aedeagus: lacking parameres, the main-piece characteristically shaped and not strongly arcuate basally. Additionally, in males of these three genera the last abdominal sternum lacks a strut—clearly a derived condition, probably associated

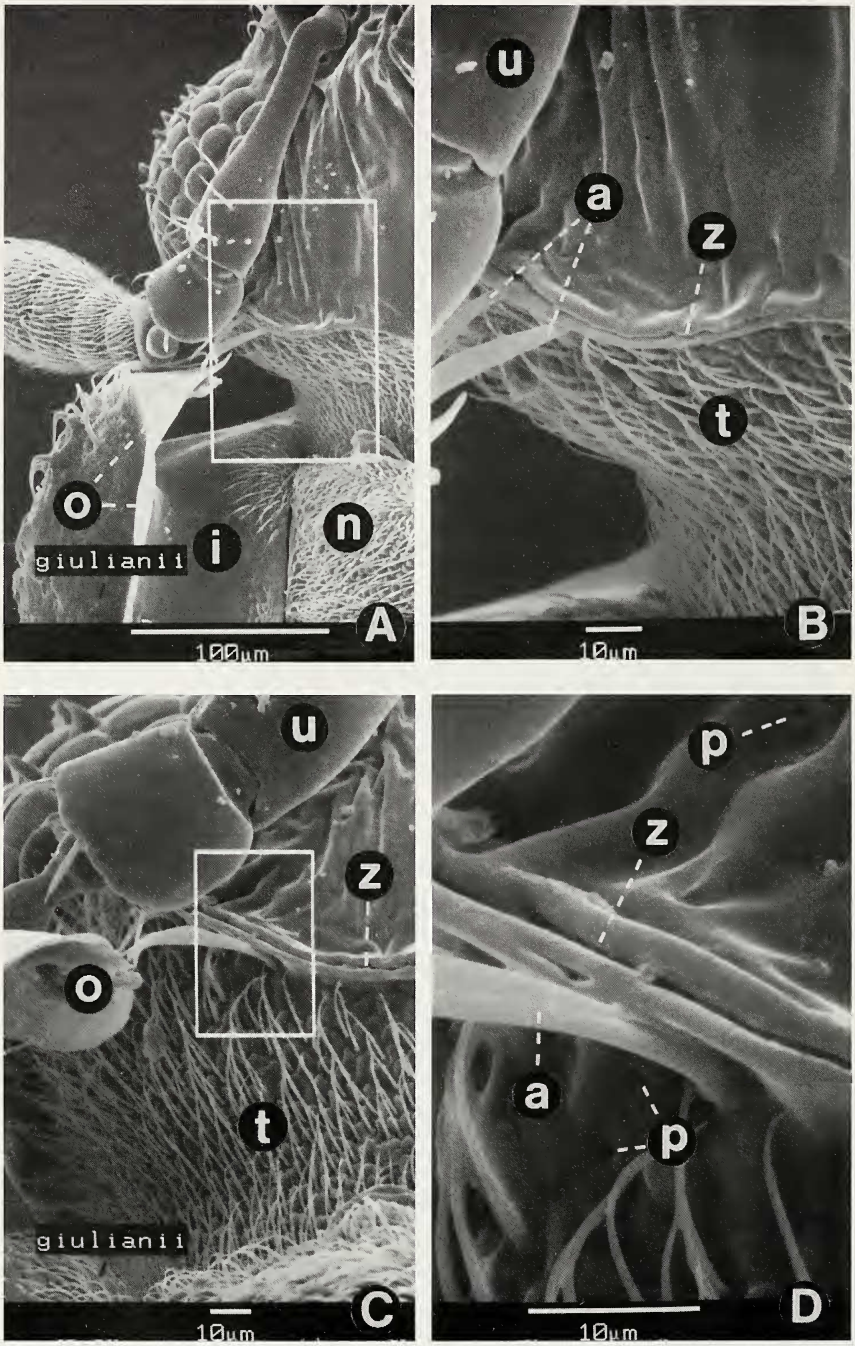


Fig. 40.—*Hughleechia giulianii*. A. Venter of head and prothorax, right side. B. Rectangular area of A, enlarged. C. Postocular area, posteroventral aspect. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (i) hypomeral antennal pocket, (n) prosternum, (o) hh-border, (p) exocrine pores, (t) postocular asperite hydrofuge, (u) first antennomere, (z) transgenal exocrine secretion sulcus.

with aedeagal morphology; all other Hydraenidae have a strut. In females the last sternum (seventh visible) is either completely concealed beneath the sixth, or with only the distal margin exposed.

Tympallopatrum and *Tympanogaster* share a distinct derived condition of the antenna: the second article is large and its distal end forms a cupule into which fits the following article and (partially so) the preclub article. The preclub article (morphological article number 6), cupuliform in most Hydraenidae, is only very marginally so (if at all) in *Meropathus,* and not at all cupuliform in *Tympallopatrum* and *Tympanogaster.*

It appears that the dorsal vestiture and sculpture morphocline in the Meropathina proceeds from a strongly setose condition, such as is present in large-bodied members of the *novicius* group of *Tympanogaster,* toward a less roughly sculptured condition, and finally to the very smooth and small-bodied members of the *deanei* group of *Tympanogaster.*

Ecologically, the Meropathina cline apparently began with fungus dwelling, proceeded to litter dwelling, then to inhabiting mossy margins of aquatic habitats such as waterfalls, and finally to mossy downstream sides of rocks and other splash-zone aquatic microhabitats. This ecocline corresponds with the morphocline of increasingly smooth dorsal sculpture.

Members of the genus *Meropathus* are discussed by Perkins (1981). The placement of some eastern Australian and Tasmanian species in *Meropathus* by Janssens (1967) and Bameul (1989) are in error; these species will be properly placed elsewhere, within the context of a generic revision.

Genus *Meropathus* Enderlein
(Fig. 41)

Meropathus campbellensis Brookes, a nonaquatic species from Campbell Island, lacks components of the specialized ESDS.

The eyes of this species are reduced, but the approximate former outline of the posteroventral angle is clearly revealed by the line of periocular pores (Fig. 41: e). The postocular hydrofuge (Fig. 41:t) is well developed and of the asperite type. Exocrine pores (Fig. 41:p) are moderately dense within the hydrofuge near its anterior limit in the genal area.

The hypomeral antennal pocket (Fig. 41:h) is very weakly developed and asperite–hydrofuge, except a smooth narrow lateral margin that is wider anteriorly. The free edge of this lateral margin forms a stiff ridge that does not have a hyaline margin; this ridge is continuous with the (wider) anterior and posterior hyaline borders. The wet-hypomeron is absent. The profemor has a distal spine cluster.

Tympallopatrum, **new genus**
(Fig. 42, 43)

Type Species.—*Tympallopatrum longitudum,* new species.

Diagnosis.—Recognized among Ochthebiinae by the eight-articled antenna (three + club) having the second article apically cupuliform, the prominent ocelli located near the eyes, the basomedial tumidity of the frons behind which are three longitudinal carinae, the transversely convex and setose dorsum, the shape of the mentum, the gular ridge, the median metasternal impression, the lack of a lateral hyaline border, and features of the antennal pocket.

Description.—**Antennal pocket.** The postocular area has a distinctive transgenal ridge (Fig. 42:r)

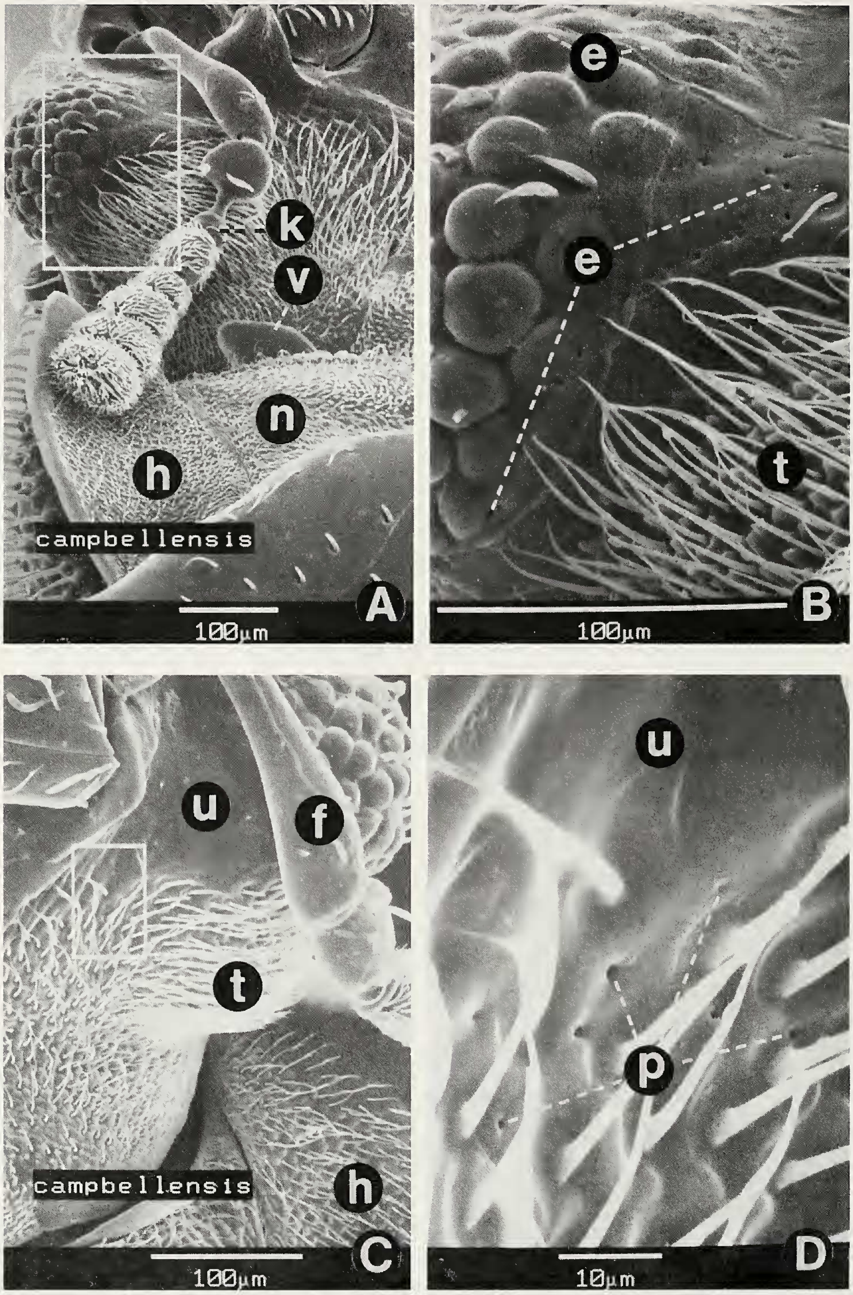


Fig. 41.—*Meropathus campbellensis.* A. Head and prothorax, posteroventral aspect of right side. B. Rectangular area of A, enlarged. C. Venter of head and prothorax, left side. D. Rectangular area of C, enlarged. Structures: (e) periocular exocrine pores, (f) first antennomere, (h) hydrofuge hypomeron, (k) cupule article of antenna, (n) prosternum, (v) cervical sclerite.

adjacent to the posteroventral angle of the eye. The postocular hydrofuge (Fig. 43:t) is moderately dense and of the asperite type, whereas the genal pubescence (hydrofuge?; Fig. 42:p, 43:p) is sparse, nonasperite, and has few exocrine pores. Periocular pores (Fig. 42:e, 43:e) are present.

The hypomeral antennal pocket is moderately well developed, the medial half hydrofuge pubescent (asperite type), the lateral half nonpubescent and weakly microreticulate (Fig. 42A:i, 43A). The lateral margin of the antennal pocket forms a ridge, but its free edge does not extend to form an hh-border; this ridge is continuous with the ah-border, but is not continuous with the ph-border. The wet-hypomeron is quite small, consisting of tuberculate enlargements upon which are placed setae. The (presumed) antennal cleaner of the prosternum is well developed (Fig. 42:a, 43B:a). The profemur has large spines over most of the upper surface; these spines are not organized to form a distal spine cluster.

Other characters. Form transversely convex. Dorsal reliefs strongly setose, including frons tumidity, ocelli, four longitudinal sinuate costae on pronotum, and four costae on elytra (on even-numbered interseries, costae often interrupted). Ocelli prominent, located next to eyes. Frons with basomedial tumidity, separated from ocelli by longitudinal sulcus; three strong parallel longitudinal carinae behind tumidity. Antennomeres eight (three + club); second cupuliform, third very small, not cupuliform. Maxillary palpi short, ochthebiine. Labrum deflexed. Mentum longer than wide. Gula with a prominent transverse ridge. Pronotum with disc transversely convex, bearing four sinuate setose costae; anterior and posterior hyaline borders narrow, bearing tiny cuticular processes; lateral margins arcuate, denticulate, and setose, lacking hyaline border, sometimes minutely excavate near posterior angles. Elytra with ten series of punctures, suture and even-numbered interseries at least in part costate and setose. Prosternum narrow in front of procoxae, with low midlongitudinal carina. Hypomeron with carina forming margin of antennal pocket. Metasternal disc shining, with median impression. Intercoxal sternite small, triangular. Legs short, tarsi very short, five–five–five. Hydrofuge pubescence present on postocular area, bubble-hypomeron, notal postcoxal projection, mesosternum, narrow band around shining metasternal area, first abdominal sternum, and narrow lateral band of abdominal sterna two to five.

Etymology.—Greek, *tympa* (from *Tympanogaster*), plus *allo* (other), plus *patrum* (country, walk): "walk to a different drummer"; gender neuter.

Tympallopatrum longitudum, new species

Type Material.—Holotype male, deposited in MCZ, and 12 paratypes with data: Western Australia, Pemberton, x.1931, P. J. Darlington, (MCZ; some to be deposited in ANIC and CMNH). Additional paratypes: M. V. "Agios Nikolaos III," Fremantle F67 [quarantine interception], 15.x.1976, (5 ANIC). Western Australia, 48 km N Albany, Porongurup Nat. Pk., 24.xii.1976, litter under karri and Acacia at head of Bolganys Creek, FMHD #76-530, J. Kethley, (49 FMNH; some to be deposited in ANIC, CMNH, and MCZ).

Description.—Size (mm × 100; length/width): body 152/66, head 30/42, pronotum 39/54, elytra 104/66. Color brown. Labrum deflexed, wider than long, in males with small dentiform median process and basomedian fovea, in females simple. Frons and clypeus setose, more densely so laterally. Pronotal disc with anterior midlongitudinal fovea, between setose costae, distinctly longer than but only slightly wider than fovea behind it, low relief between foveae very weakly developed; punctures in anterior fovea forming two short longitudinal series; two granules at margin of each pronotal puncture. Pronotal lateral margin granulose and setose, arcuate, minutely excavate at posterior angles. Elytra nearly parallel-sided, flat on disc, with ten quite regular series of punctures; costae straight, present on even-numbered intervals as follow: second: interrupted over short distance slighlty past midlength; fourth: interrupted over short distance in apical fourth, joining with second slightly before apices; sixth: ended near distal fourth; eighth: ended just before place where second and fourth become confluent. Elytral margin minutely granulate and setose. Hypomeron with antennal pockets wide, dull; wet-hypomeron very narrow, present only in posterior half. Metasternal disc shining, with nearly parallel-sided midlongitudinal sulcus from base to anterior fourth where joins low midlongitudinal carina.

Etymology.—Latin, *longitudum* (length, longitude), a reference to longitudinal orientation.

Discussion.—A figure of the male genitalia of *T. longitudum,* and descriptions of additional new species in the genus, will be given in a separate paper.

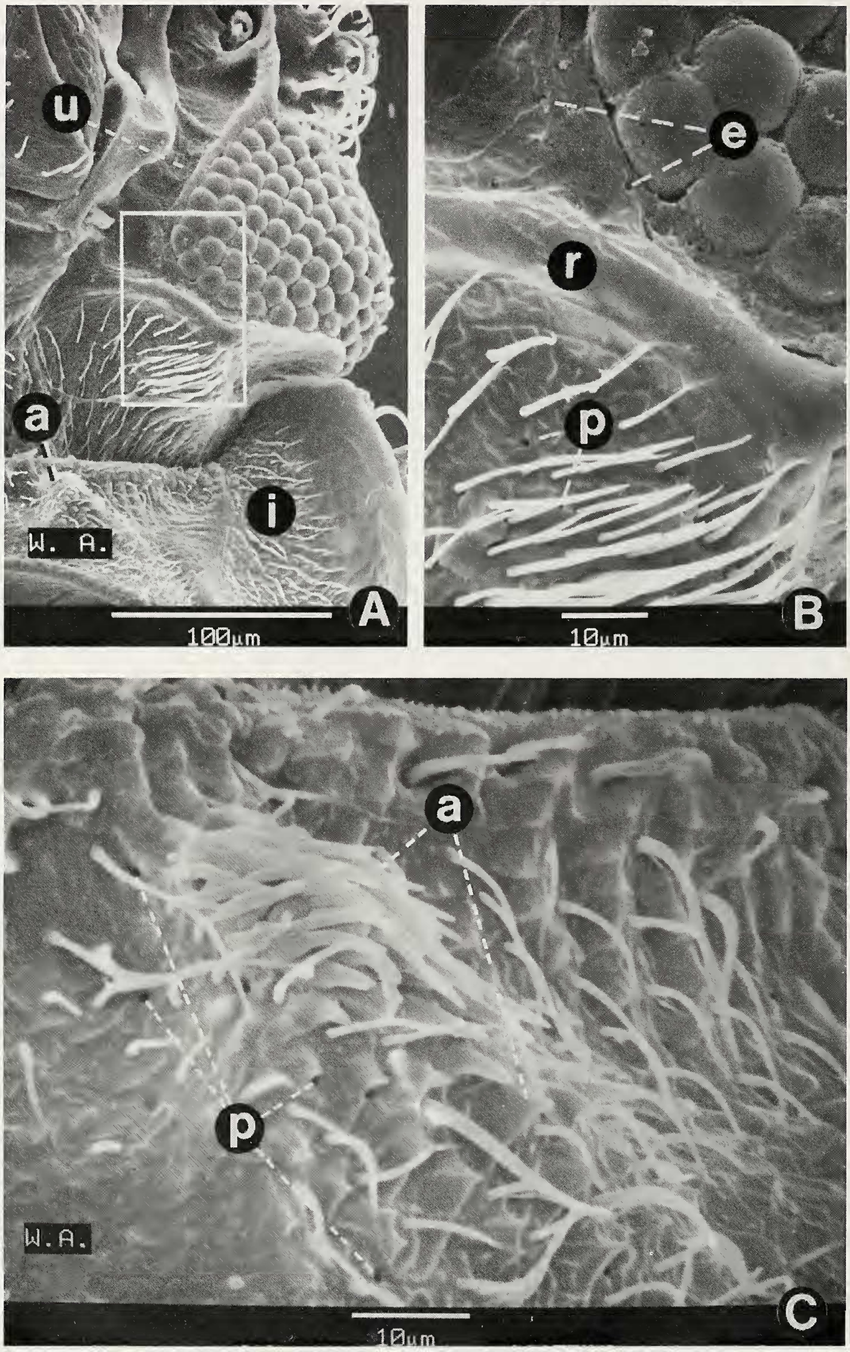


Fig. 42.—*Tympallopatrum longitudum.* A. Head and prothorax, posteroventral aspect of left side. B. Rectangular area of A, enlarged. C. Prosternum. Structures: (a) antennal cleaner, (e) periocular exocrine pores, (i) hypomeral antennal pocket, (p) exocrine pores of gena, (r) genal ridge, (u) subocular antennal groove.

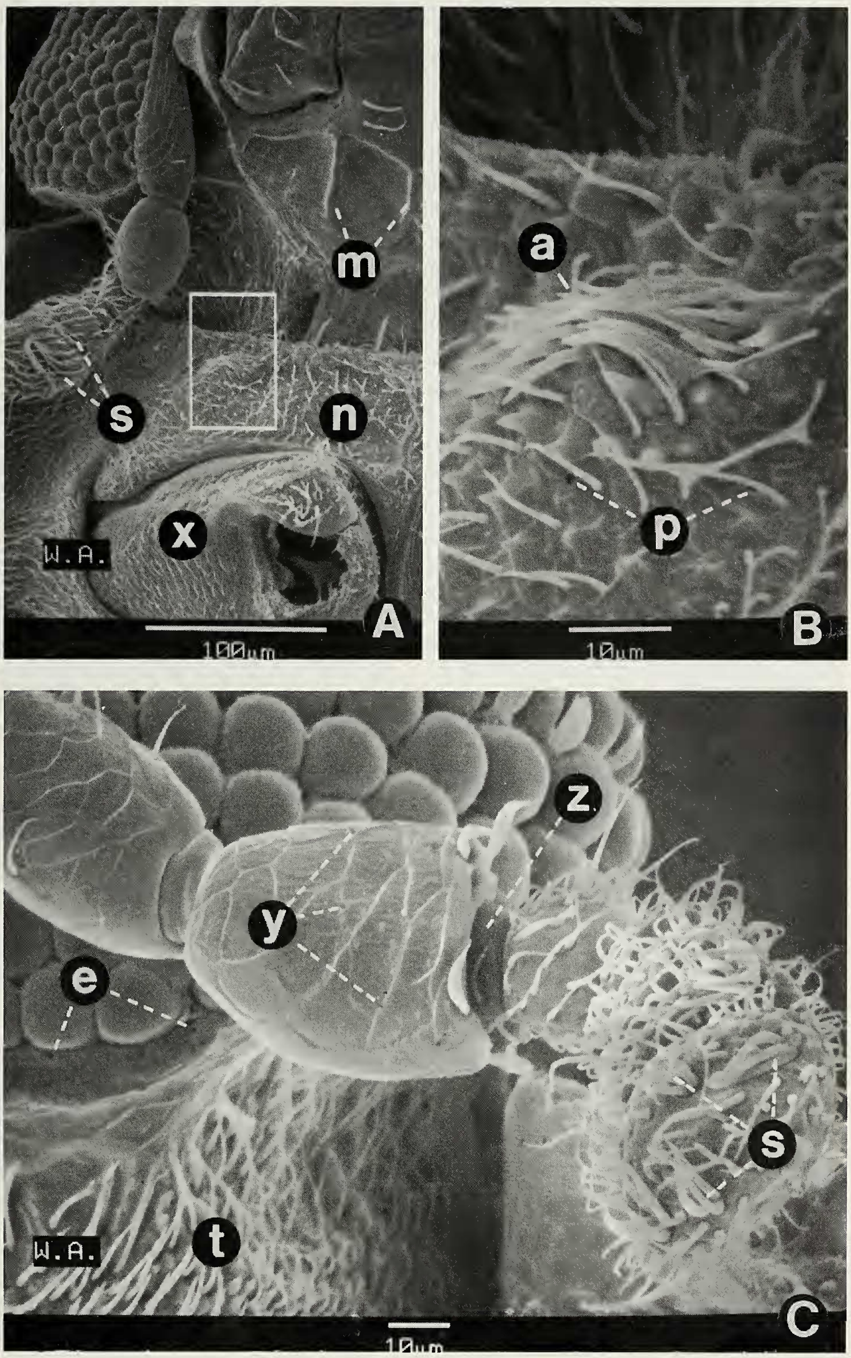


Fig. 43.—*Tympallopatrum longitudum.* A. Venter of head and prothorax, right side. B. Rectangular area of A, enlarged. C. Antenna and adjacent postocular area. Structures: (a) antennal cleaner, (e) periocular exocrine pores, (m) submental ridges, (n) prosternum, (p) exocrine pores, (s) sensilla of antennal club, (t) postocular asperite hydrofuge, (x) procoxa, (y) exocrine pores of second antennomere, (z) third antennomere.

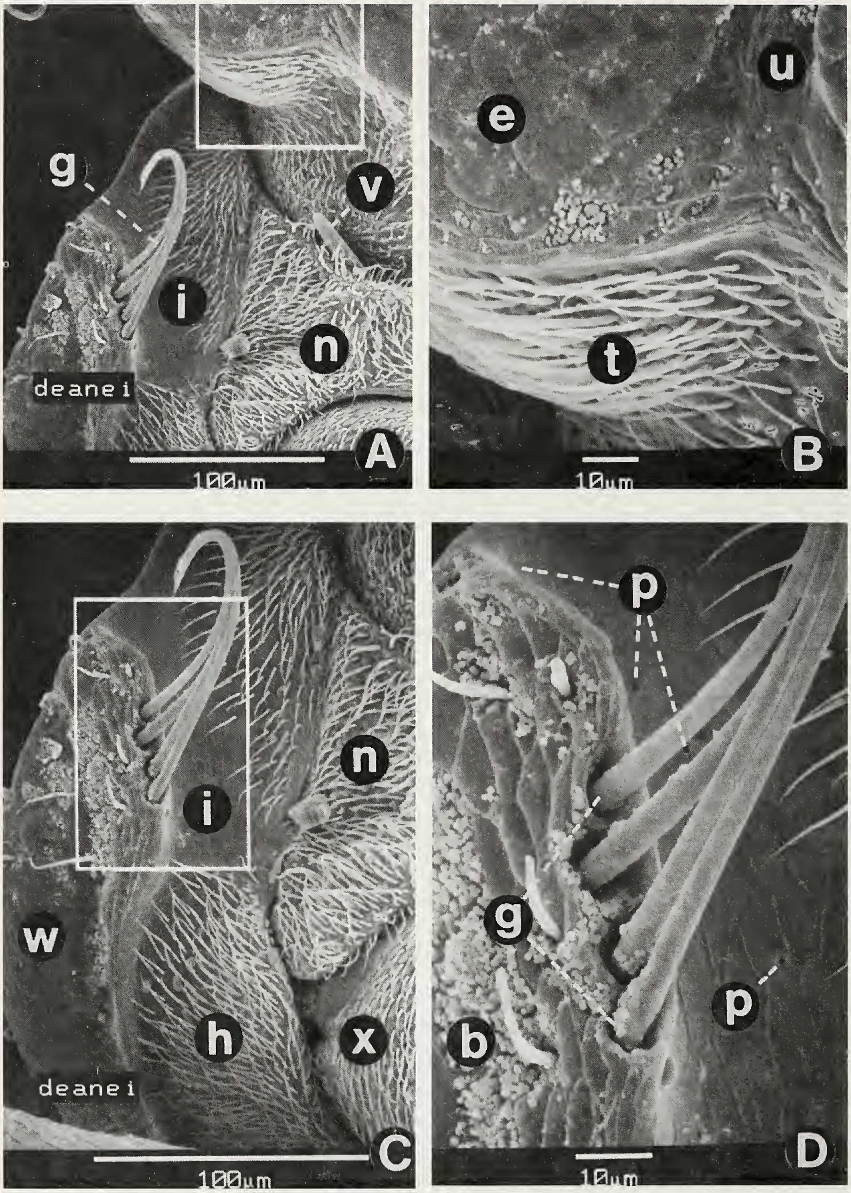


Fig. 44.—*Tympanogaster deanei.* A. Postocular and adjacent prothoracic areas, right side. B. Rectangular area of B, enlarged. C. Venter of prothorax, right side. D. Rectangular area of C, enlarged. Structures: (b) bacteria(?), (g) hap-setae, (h) hydrofuge hypomeron, (i) hypomeral antennal pocket, (n) prosternum, (p) exocrine pores of antennal pocket, (t) postocular hydrofuge, (u) subocular antennal groove, (v) cervical sclerite, (w) wet-hypomeron, (x) procoxa.

Tympanogaster Janssens
(Fig. 44, 45)

Discussion.—Members of *Tympanogaster,* an Australian and Tasmanian genus, lack a specialized ESDS. Representatives of two distinct species groups were

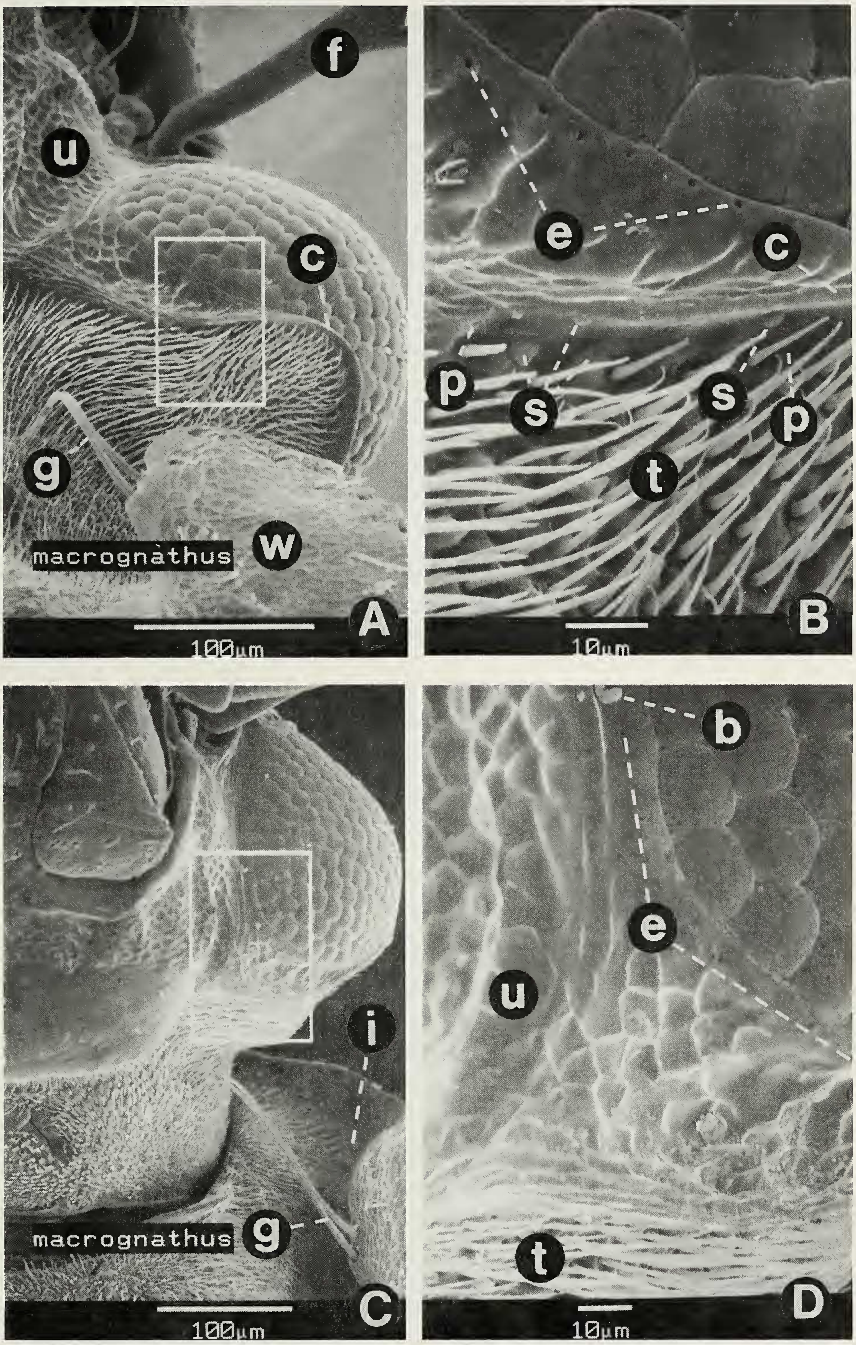


Fig. 45.—*Tympanogaster macrognathus.* A. Postocular and adjacent prothoracic areas, posteroventral aspect of left side. B. Rectangular area of A, enlarged. C. Ventral aspect of head and adjacent prothorax, left side. D. Rectangular area of C, enlarged. Structures: (b) bacteria(?), (c) postocular carina, (e) periocular exocrine pores, (f) first antennomere, (g) hap-setae, (i) hypomeral antennal pocket, (p) exocrine pores, (s) presumed exocrine secretion, (t) postocular hydrofuge, (u) subocular antennal groove, (w) wet-hypomeron.

studied, *T. deanei* Perkins (*deanei* group) and *T. macrognathus* (Lea) (*macrognathus* group). Members of the *macrognathus* group have been incorrectly placed in the genus *Meropathus* by Janssens (1967) and Bameul (1989). This genus is currently being revised by the author; additional study is needed to determine if a new genus is warranted for the *macrognathus* group.

Description.—**Antennal pocket.** The postocular area has a distinct transgenal ridge that is a continuation of an orbital ridge (Fig. 44B:c, 45:c). The postocular hydrofuge is short and dense (asperite type; Fig. 44:t, 45:t), with sparse exocrine pores near the orbital ridge (Fig. 45:p), and presumed exocrine secretions (Fig. 45:s). Periocular pores are present (Fig. 45:e).

The hypomeral antennal pocket (Fig. 44:i, 45:i) is well developed. In *T. macrognathus* it has a smooth, nonpubescent surface, except for the anteromedial area that is hydrofuge pubescent (Fig. 45C), whereas in *T. deanei* the pocket is hydrofuge pubescent over about the medial half (Fig. 44C), the remainder being nonpubescent, weakly microreticulate, and having sparse exocrine pores (Fig. 44D:p).

The hypomeral antennal pocket setae (Fig. 44:g, 45:g) differ in the two species groups, consisting of two setae in the *macrognathus* group (Fig. 45) and four in the *deanei* group (Fig. 44). The wet-hypomeron (Fig. 44:w, 45:w) is large, and separated from the bubble-hypomeron by a well-developed hypomeral carina.

The hh-border and lh-border are absent. The ah-border, when present, is extremely narrow; in some specimens it is absent, perhaps abraded away by movements of the head (e.g., Fig. 45C). The ph-border, when present, is extremely narrow and limited to about the middle quarter of the base; in some specimens it is absent. The profemur is armed with spines on the upper, distal surface, but these spines are very short, about the same length as other spines on the profemur, and are not organized into a discrete distal spine cluster.

Subtribe Neochthebina, **new subtribe**

This monotypic subtribe is erected for the genus *Neochthebius*. The postocular area and hypomeron are plesiomorphic, and hyaline borders are absent. The antenna has the derived condition, relative to the Meropathina, of a cupuliform preclub (anatomical fourth) article.

Neochthebius Orchymont

(Fig. 46, 47)

Neochthebius vandykei (Knisch), an intertidal species from western North America, lacks all components of the specialized exocrine secretion delivery system. The absence of the specialized ESDS components corroborates the elevation of *Neochthebius* from subgeneric to generic status (Perkins, 1981).

The postocular area has well-developed periocular pores (Fig. 46:e, 47:e). The periocular pore area at the posteroventral angle of the eye is comparatively wide and the adjacent facets are comparatively flattened, both conditions reflecting the reduced eye size. The postocular hydrofuge area is of the asperite type, and has sparse exocrine pores (Fig. 46:p, 47:p).

The hypomeral antennal pocket (Fig. 46:i, 47:i) is moderately developed, microreticulate throughout (no smooth lateral band), and lacks hydrofuge pubescence except for a small patch of setae at the anteromedial extreme. The hh-border and lh-border are entirely absent, whereas the ah-border and ph-border are present. The profemur lacks a distal spine cluster.

Subtribe Protochthebiina, **new subtribe**

This subtribe is erected for the genus *Protochthebius*. The postocular area in this subtribe is plesiomorphic, and the hypomeron has a hypomeral hyaline border with horizontal (plesiomorphic) orientation, but lacks a lateral hyaline border.

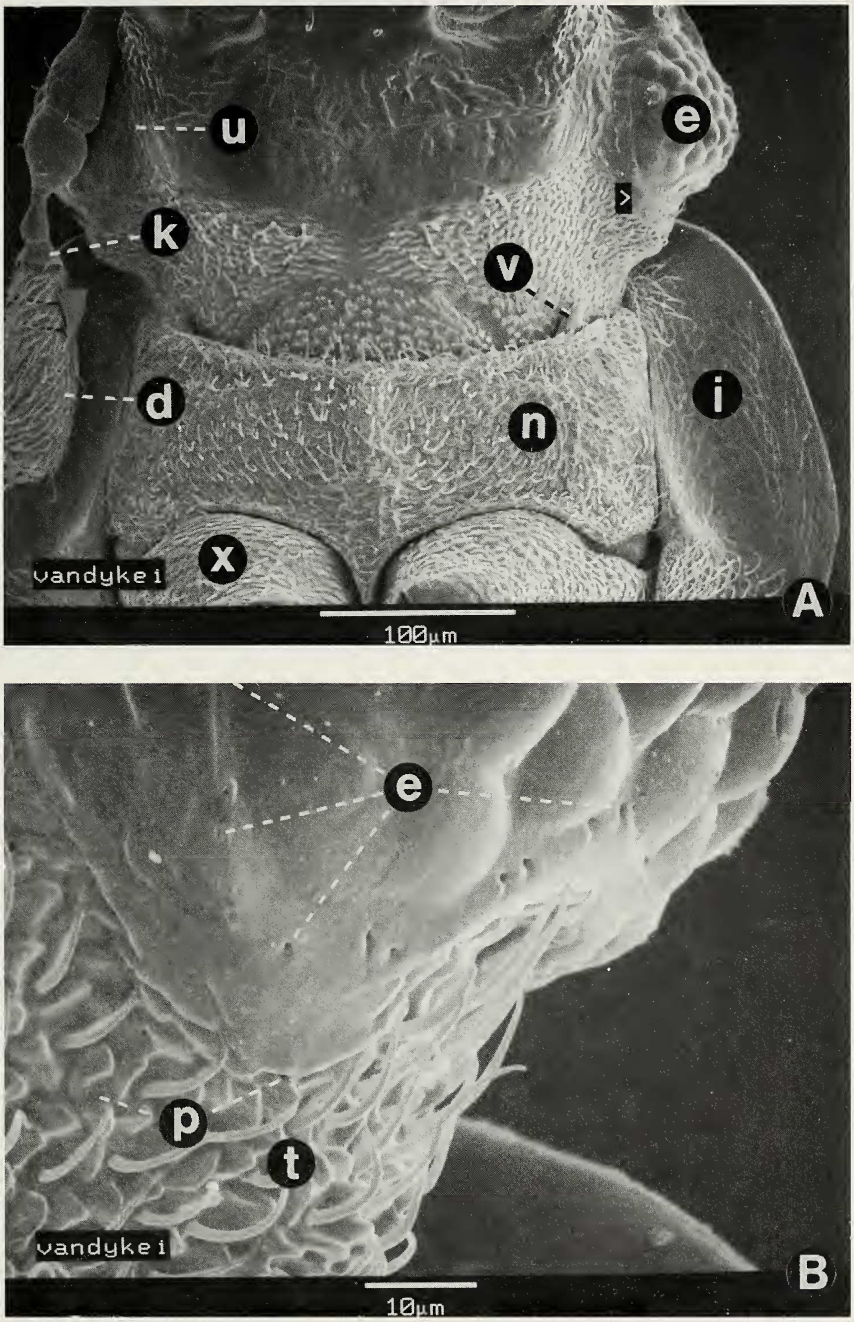


Fig. 46.—*Neochthebius vandykei.* A. Venter of head and prothorax. B. Postocular area. Structures: (d) antennal club, (e) eye and periocular exocrine pores, (i) hypomeral antennal pocket, (k) cupule article of antenna, (n) prosternum, (p) exocrine pores, (t) postocular asperite hydrofuge, (u) subocular antennal groove, (v) cervical sclerite, (x) procoxa.

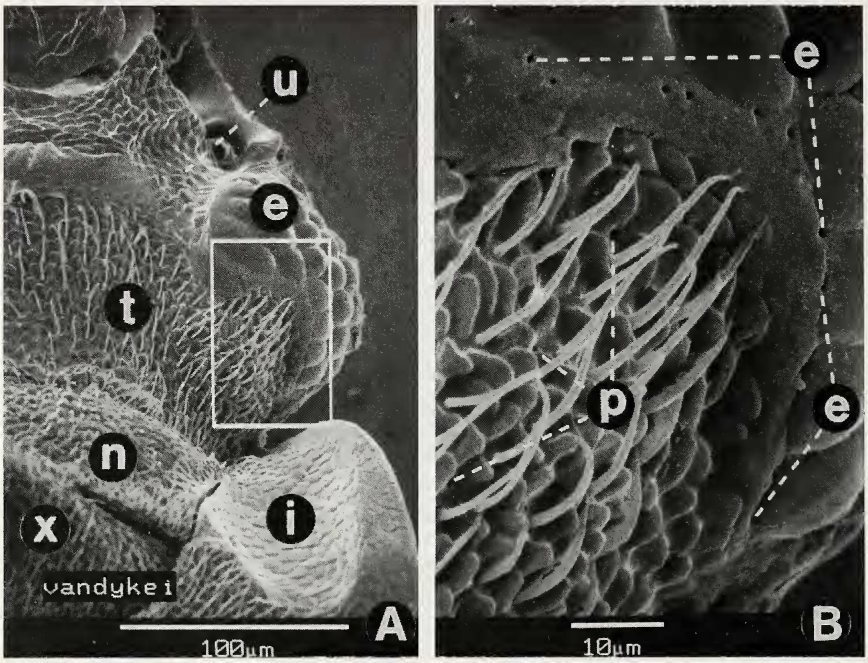


Fig. 47.—*Neochthebius vandykei.* A. Head and thorax, posteroventral aspect of left side. B. Rectangular area of A, enlarged. Structures: (e) eye and periocular exocrine pores, (i) hypomeral antennal pocket, (n) prosternum, (p) exocrine pores of postocular asperite hydrofuge, (t) genal asperite hydrofuge, (x) procoxa.

Protochthebius, **new genus**

(Fig. 48, 49)

Type Species.—*Protochthebius satôi,* new species.

Diagnosis.—Recognized among Ochthebiini by the nine-articled antenna (four + club) having the second article oval, the third slender and elongate, length subequal to combined lengths of the first three articles of the club, the fourth article cupuliform; the postocular area lacking secretion distribution setae; the antennal pockets of the hypomeron microreticulate and pubescent; the hypomeral hyaline border located at the lateral margin of the hypomeron (wet-hypomeron absent), in a horizontal plane and visible dorsally at posterior sides of pronotum; and the lateral hyaline border absent.

Description.—**Antennal pocket.** The postocular area near the posteroventral angle of the eye lacks secretion delivery setae and also lacks the associated secretion sulcus. There is, however, a transgenal sulcus (Fig. 48:c), perhaps with exocrine pores. This sulcus may represent the primitive condition from which were derived the various forms of secretory sulcus seen in *Ochthebius, Gymnochthebius, Aulacochthebius,* and *Hughleechia.* The periocular pores (Fig. 48:e) are well developed and the postocular hydrofuge (Fig. 48:t, 49:t) is dense and of the asperite type.

The prothoracic hypomeron has a very shallow antennal pocket that is entirely hydrofuge pubescent. The pubescence is borne on a microreticulate surface of distinctive pattern (Fig. 48:i, 49:i). Interspersed in this microrecticulate pattern are exocrine pores. The hypomeral antennal pocket is margined laterally with a smooth border that, at its lateral extreme, becomes the hh-border (Fig. 48:o, 49:o). The hh-border is approximately in a horizontal plane, and becomes wide enough posteriorly to be seen in dorsal aspect. The hh-border is contiguous anteriorly and posteriorly with the ah-border and ph-border, respectively.

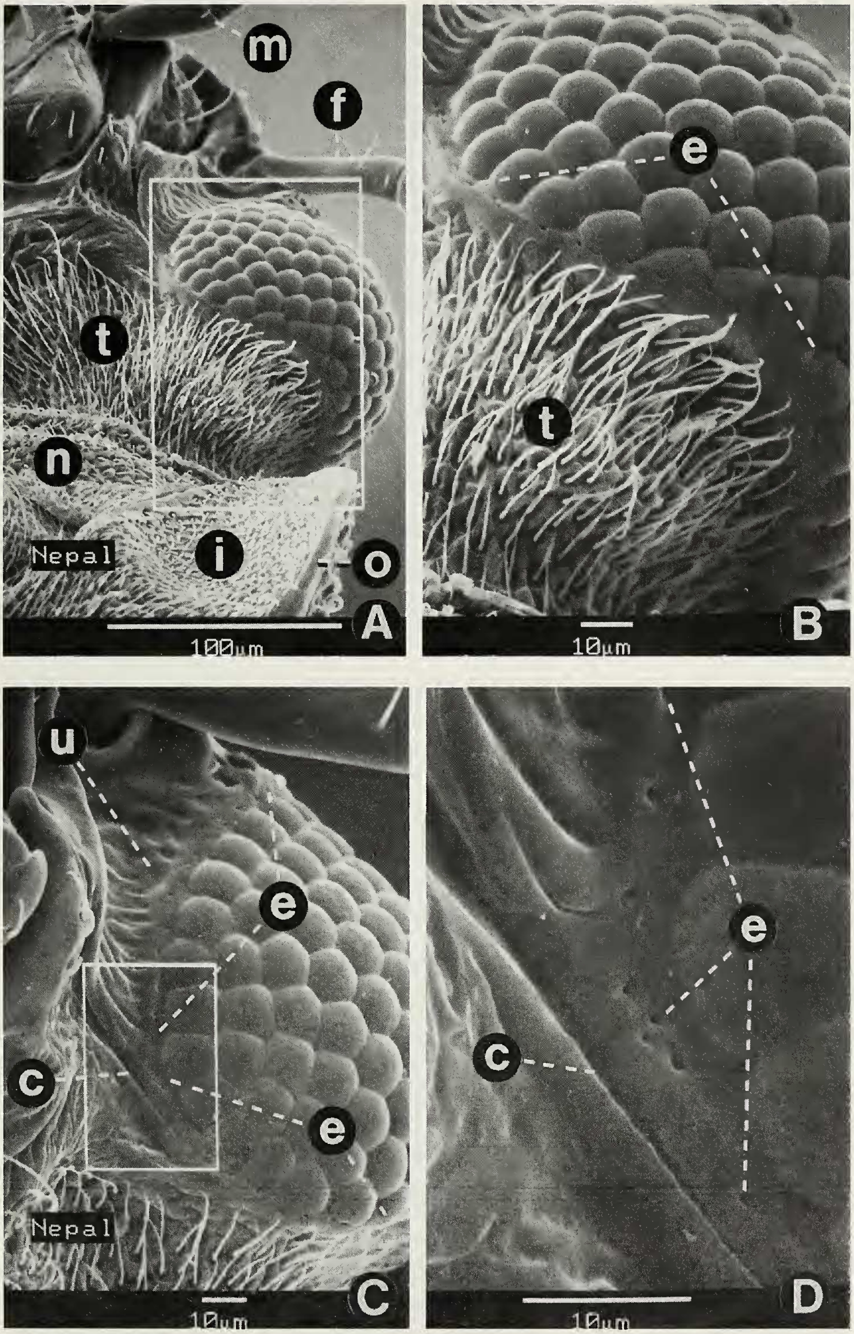


Fig. 48.—*Protochthebius satôi*. A. Head and prothorax, posteroventral aspect of left side. B. Rectangular area of A, enlarged. C. Periocular area, ventral aspect. D. Rectangular area of C, enlarged. Structures: (c) subocular secretion sulcus, (e) periocular exocrine pores, (f) first antennomere, (i) hypomeral antennal pocket, (m) maxillary palpus, (n) prosternum, (o) hh-border, (u) subocular antennal groove.

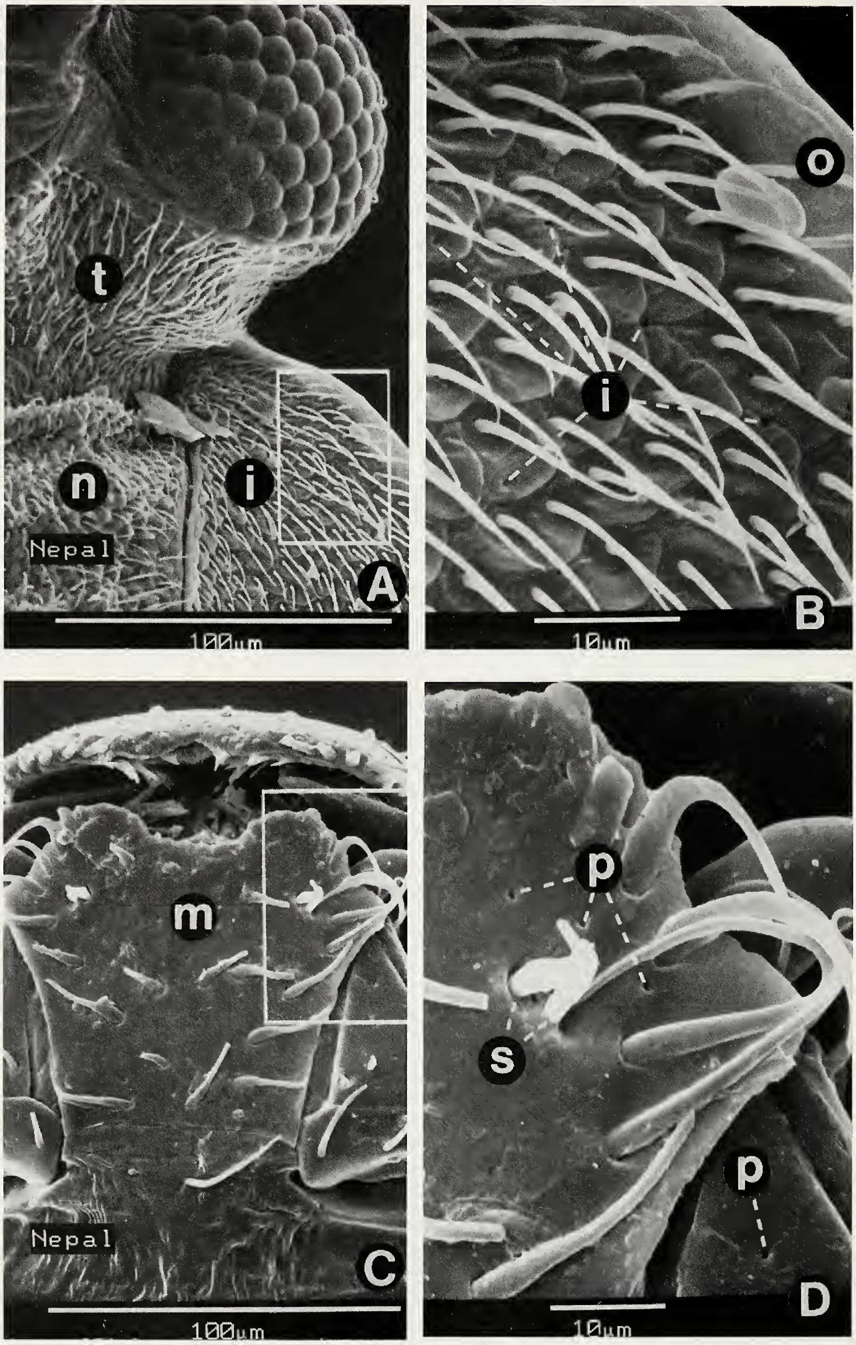


Fig. 49.—*Protochthebius satôi.* A. Venter of head and prothorax, left side. B. Rectangular area of A, enlarged. C. Mentum. D. Rectangular area of C, enlarged. Structures: (i) hypomeral antennal pocket and exocrine pores, (m) mentum, (n) prosternum, (o) hh-border, (p) exocrine pores, (s) mental sensilla, (t) genal hydrofuge.

The wet-hypomeron is absent (the hh-border being located at the lateral extreme of the hypomeron). An lh-border is absent. However, the prothorax is narrowed at the base, and in dorsal aspect the hh-border is visible in this area, and can be misinterpreted as the lh-border. The profemur does not have a distal spine cluster.

Other characters. Size small, about 1.22 mm long, form moderately elongate, moderately transversely convex. Dorsal setae weakly developed. Ocelli located near eyes. Antennomeres nine (four + club); second oval, third slender and elongate, length subequal to combined lengths of first three articles of club, fourth article cupuliform. Maxillary palpi short, length ratios of articles two to four as one : four : one, third article twice width of fourth (last). Labrum moderately deflexed from plane of clypeus. Pronotal disc with midlongitudinal sulcus and two admedian foveae on each side; lateral depressions well developed. Anterior and posterior hyaline borders narrow. Elytra with ten series of punctures. Prosternum and procoxae about equal in length. Antennal pockets of hypomeron wide, shallow, microreticulate, and pubescent. Hypomeral hyaline border postioned laterally (wet-hypomeron absent), in horizontal plane, visible dorsally at posterior sides of pronotum; lateral hyaline border absent. Metasternal disc moderately convex, lacking impressions. Intercoxal sternite small, triangular. Legs short, tarsi short, five–five–five. Hydrofuge pubescence present on postocular area, hypomeron, notal postcoxal projection, mesosternum, metasternum, and first five visible abdominal sterna.

Etymology.—Greek, *proto* (first), plus *Ochthebius*; gender masculine.

Protochthebius satôi, **new species**

Type Material.—Holotype male: Nepal, Sindhu, Lamosangu, 900m, 18–21.x.1979, M. Satô leg.; deposited in NSMT. Forty-five paratypes with same data as holotype; deposited in CMNH, FMNH, MCZ, and MSC.

Description.—Size (mm × 100; length/width): body 122/53, head 27/33, pronotum 27/39, elytra 78/53. Color black, antennae brown. Dorsum entirely dull, with dense micropunctulate ground sculpture plus, on frons and pronotum, larger secondary punctation giving subrugulose surface. Labrum wider than long, apicomedially emarginate in both sexes. Frons with two well-developed foveae. Pronotal disc with midlongitudinal sulcus that is shallowest in the middle, giving the impression of two foveae, one behind the other; two foveae on each side of sulcus, one behind the other, the posterior nearly twice as large as the anterior; lateral depressions well developed. Pronotal lateral margins strongly arcuate before middle, constricted behind, where is visible hypomeral hyaline border. Elytra transversely convex, longitudinally flat on disc, with ten very regular series of relatively large punctures, slightly larger than width of intervals, and closely spaced longitudinally, each puncture with a minute seta; intervals very slightly rounded. Elytral margin narrowly explanate. Metasternal disc dull, entirely microreticulate, and hydrofuge pubescent.

Etymology.—I am pleased to dedicate this new species to Masataka Satô, fellow aquatic coleopterist who collected the type series.

Discussion.—A figure of the male genitalia of *P. satôi,* and descriptions of additional new species in the genus, will be given in a separate paper.

Subtribe Enicocerina, **new subtribe**

This subtribe is erected for *Enicocerus* Stephens. The postocular area has a secretion shelf, behind which are short brush-like secretion distribution setae that can be contacted by the wide anterior extreme of the hypomeral hyaline border. The hap-setae are short compared to the width of the hypomeral hyaline border. The prothorax has anterior, posterior, hypomeral, and lateral hyaline borders.

Enicocerus Stephens, **new status**
(Fig. 50; 51A, B)

Discussion.—The following description is based on SEM and transparency mounts of *E. exsculptus* and transparency mounts of *E. benefossus.*

Description.—**Antennal pocket.** The postocular pores are located in the same area as those of *Ochthebius* (at the posteroventral angle of the eye) but instead of being in a secretion sulcus the pores are distributed on a smooth area, the postocular secretion shelf (Fig. 50:p).

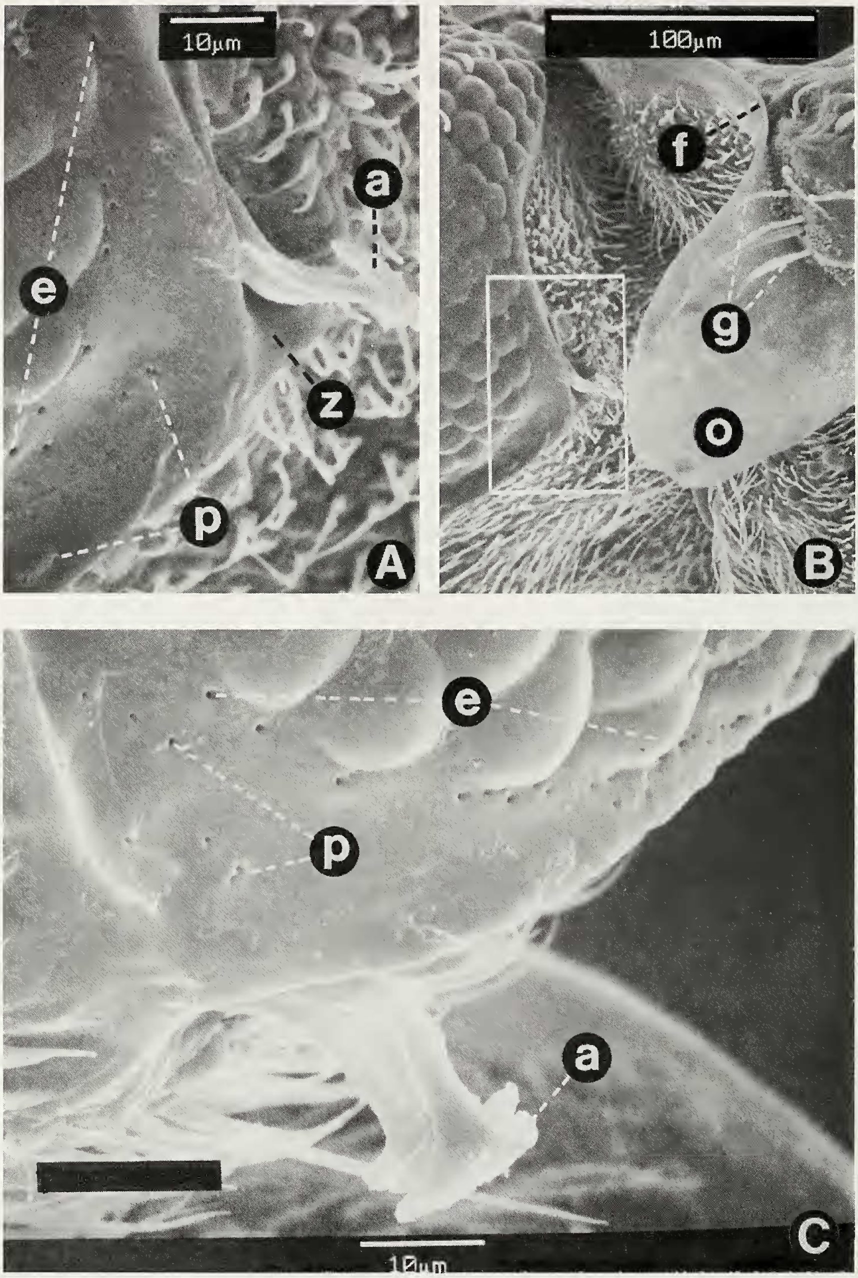


Fig. 50.—*Enicocerus exsculptus*. A. Rectangular area of B, enlarged. B. Postocular and adjacent prothoracic areas, lateral aspect. C. Postocular exocrine pore area. Structures: (a) psd-setae, (e) periocular exocrine pores, (f) ah-border, (g) hap-setae, (o) hh-border, (p) pores on postocular exocrine secretion distribution surface, (z) cuticular ridge.

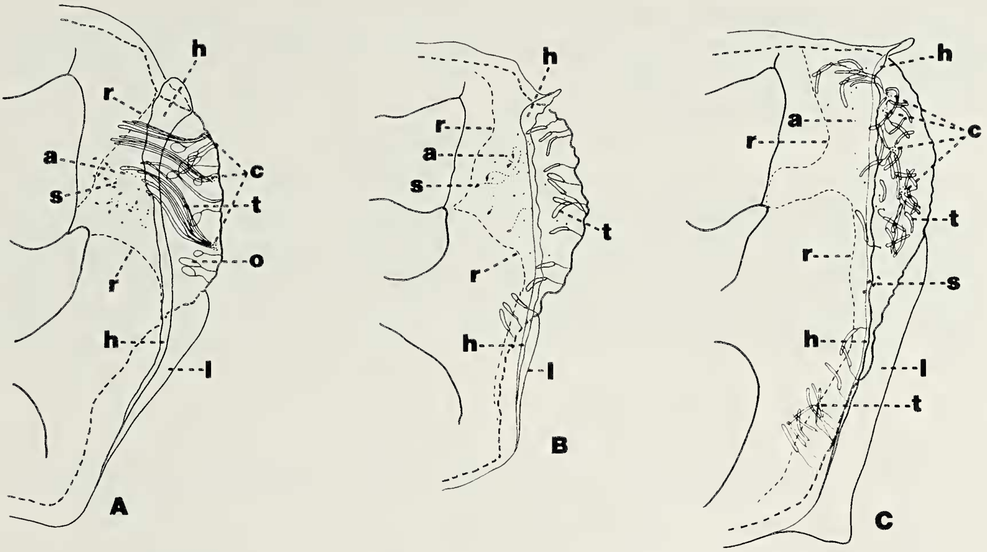


Fig. 51.—Ventral aspect of prothorax, left side, showing three types of internal end-apparatus, exocrine pore locations, and hyaline borders (setae omitted). A. *Enicocerus exsculptus.* B. *E. benefossus.* C. *Gymnochthebius plesiotypus.* Structures: (a) single exocrine pores of antennal pocket, (c) exocrine pore clusters on wet-hypomeron, (h) hh-border, (l) lh-border, (o) sacoid end-apparatus, (r) lateral limit of hypomeral hydrofuge setae, (s) spermoid end-apparatus, (t) tubuloid end-apparatus.

The psd-setae, instead of long and tapering as in *Ochthebius,* are short and expanded apically to form stout brush-like tips (Fig. 50:a). These specialized setae are supported at their bases by a cuticular ridge (Fig. 50:z). The periocular pores are well developed (Fig. 50:e). The postocular hydrofuge is short, dense, and asperite.

The hypomeral antennal pocket is well developed, hydrofuge pubescent anteromedially. The hh-border is large at its anterior extreme and the hypomeral antennal pocket setae are relatively short (Fig. 50:o, g). Consequently, the hh-border and not the pocket setae would be in a position to contact the postocular setae, a condition opposite that of *Ochthebius.* The ah-border and hh-border are contiguous (Fig. 50:f). The lh-border is well developed, contiguous with the ph-border, and across its ventral surface passes the hh-border. The profemur has a distal spine cluster, the spines of moderate length.

The hypomeral exocrine glands of *E. exsculptus* (Fig. 51A) are well developed and comprise three types, based on shape of the end-apparatus: (1) spermoid—sperm-shaped (similar to those in Fig. 3), with long ductules relative to the size of the end-apparatus (Fig. 51:s); the pores (Fig. 51:a) for these glands are solitary, and are present principally in the nonhydrofuge pubescent part of the hypomeral antennal pocket; (2) "tubuloid"—tubule-shaped, with short ductules relative to the length of the end-apparatus (Fig. 51:t); the pores of the majority of these glands are grouped into three distinct clusters (Fig. 51:c) on the wet-hypomeron, each cluster comprised of about eight pores; and (3) "saccoid"—oval or sack-shaped (Fig. 51:o), with moderately long ductules; the pores of these glands are located at or near the lateral margin of the hypomeron.

The hypomeral exocrine glands of *E. benefossus* (Fig. 51B) are much smaller than those of *E. exsculptus.* The elongate tubuloid glands of the wet-hypomeron are absent, and the glands occupying the homologous position of the saccoid glands of *exsculptus* are more tubuloid than saccoid (Fig. 51:t).

Subfamily Hydraeninae Mulsant

Tribe Hydraenini

This tribe comprises the genera *Hydraena* and *Adelphydraena.* This group, elevated from subtribal level, is characterized by the following (see also Perkins, 1989): (1) the prosternal intercoxal process is expanded laterally behind the procoxae, closing the procoxal cavities (tip of each lateral process fitting into small notch in corresponding postcoxal pronotal projection); (2) the second article of the maxillary palpus is elongate and slender; and (3) the last sternum in females has a pair of sensory clusters.

Genus *Hydraena* Kugelann

The following derived characters were given by Perkins (1989) as diagnostic for *Hydraena*: (1) mandible–labrum with interlocking structure, (2) mentum with apicomedial projection, (3) hypomeron (= proepisternum) with antennal pocket opening ventrally, and (4) antenna with nine articles. To this list can now be added the presence of the following derived characters: (1) hsd-sulcus, (2) hsd-surface, (3) dome-shaped sensilla of hypomeron, (4) gap-setae, and (5) antennal cleaner.

Subgenera of *Hydraena*

There is correspondence in the polarity of seven hypomeral morphoclines in *Hydraena.* The stepwise progression of each morphocline is represented, from ancestral to derived, by conditions present in *H.* (*Haenydra*) *gracilis* (Fig. 9A, 13A, 14A), *H.* (sensu stricto) *riparia* (Fig. 11A, 12), and *H.* (sensu stricto) *americana* (Fig. 11B, 13B, 14B). Most of these morphoclines are related to the formation and integration of the component parts of the antennal pocket.

The morphoclines involve: (1) the width of the ventral opening of the antennal pocket, (2) the locations of the hypomeral antennal pocket (hap-) setae, (3) the contact point of the hypomeral carina and the margin of the antennal pocket, (4) the degree of integration of the antennal cleaner spines, (5) the shape of the hypomeral carina, (6) the lengths of the ductules of the exocrine glands that supply the hsd-sulcus, and (7) the width and sinuosity of the hsd-sulcus.

Width of the Ventral Opening of the Antennal Pocket.—A ventrally closed antennal pocket is plesiomorphic, based on the structure of *Adelphydraena* (Fig. 52C), and other less derived genera such as *Parhydraenida.* The ventral opening, a synapomorphic character of *Hydraena* (Perkins, 1989:453), is narrowest in *gracilis* (*Haenydra*), wider in *riparia,* and wider yet in the majority of *Hydraena* (sensu stricto; both temperate and tropical).

Locations of the Hypomeral Antennal Pocket Setae.—The morphocline is: (a) present as a row of setae on the wet-hypomeron, as in *gracilis*; (b) some setae located on the anterior part of the antennal pocket (the most medial usually located on the hypomeral carina), as in *riparia*; and finally (c) the hap-setae forming a row along the margin of the antennal pocket, as in many *Hydraena* (both temperate and tropical).

Contact Point of the Hypomeral Carina and the Margin of the Antennal Pocket.—The morphocline is: (a) near the anterior extreme of the antennal pocket, as in *gracilis*; (b) slightly more posterior, as in *riparia*; and finally (c) adjacent to the antennal pocket, such that hydrofuge pubescence (abundant in this location in *gracilis,* and less so in *riparia*) is absent, as in many temperate and tropical species.

Degree of Integration of the Antennal Cleaner Spines.—The antennal cleaner morphocline proceeds from the relatively short-spined and less clustered cleaner of *gracilis* (Fig. 17C, D), to the longer-spined but not densely clustered condition of *riparia* (Fig. 16C), to the long-spined and densely clustered condition of most *Hydraena* (sensu stricto; Fig. 15A, B; 16D, 17A, B).

Shape of the Hypomeral Secretion Delivery Surface.—Primitively, as in *gracilis* (Fig. 13A, 14A), the hsd-surface is flat, very smooth, and relatively wide on each side of the hsd-sulcus; in *riparia* (Fig. 12A) the part of the hsd-surface that is medial to the hsd-sulcus is very narrow relative to the lateral part, which is slightly convex; and finally, in many species, the secretion-spreading surface is very convex and relatively narrow (e.g., Fig. 19A).

Lengths of the Ductules of the Exocrine Glands that Supply the HSD-Sulcus.—In the primitive condition, as in *gracilis* (Fig. 10A:f), the end-apparatus is relatively small and located immediately below the exocrine pores. In the intermediate condition, as in *riparia* (Fig. 11A:f), the end-apparatus is larger and slightly farther from the pores. In the most derived condition, as in *americana* (Fig. 11B:f) and *testacea* (Fig. 10B:f), the end apparatus is located at the ends of long ductules, well separated from the exocrine pores.

Width and Sinuosity of the HSD-Sulcus.—In the primitive condition the hsd-sulcus is wider and is not straight, as in *gracilis* (Fig. 14A). In the most derived condition the sulcus is extremely narrow and very straight (Fig. 13B, 18D). The relatively wide and sinuous primitive condition is probably a result of the fact that the exocrine glands are close to the pores, such that the pores must be offset slightly one from the other. This is not necessary in the derived condition, as the exocrine glands are separated from the pores by long ductules.

The direction of change of each of these morphoclines is the same as the polarity of the morphocline of increasing numbers of elytral series of punctures (Berthélemy, 1986; Perkins, 1989). These corresponding morphoclines provide very compelling evidence of the direction of morphological change in the evolution of an ecologically effective *Hydraena,* and consequently its component phylogenetic groups.

Subgenus *Haenydra* Rey
(Fig. 10A; 13A; 14A; 17C, D; 21A)

This taxon has been treated as both a genus and a subgenus, recently by the same author. The differences between the published opinions of Jäch (1988, 1992*b*) obviously result from the phylogenetic evidence and reasoning presented in the interim by Perkins (1989) and Hansen (1991). Nevertheless, Jäch (1992*b*: 79) does not cite these works in his vacillating argument, which terminates in the statement, "The question whether *Haenydra* should be treated as a subgenus or genus is merely a technical one."

Subgeneric status for *Haenydra* is well corroborated by the hypomeral structure. Having the plesiomorphic condition for all of the characters studied, it is now clear that among known, extant *Hydraena,* the *Haenydra* line is the earliest (or among the earliest) to diverge.

One might consider elevating *Haenydra* to full generic status, were it not for the fact that *Haenydra* possesses the initial stages of those features that probably contributed greatly to the "bloom" of the lineage: the ESDS, the antennal cleaner, and the postocular sensilla. Additionally, there is no strong synapomorphy for the species of "*Hydraena*" that would remain.

For these reasons, plus the other strong synapotypic characters known for *Hydraena* (sensu lato; Perkins, 1989), plus the fact that intermediate elytral configurations exist between *Haenydra* and *Hydraena* (sensu stricto), plus the monophyly inferred from the aedeagal shape and lack of parameres (Orchymont, 1930), *Haenydra* is retained as a subgenus.

Subgenus *Hadrenya* Rey

This taxon has a checkered history. Described as a subgenus of *Hydraena* by Rey (1886), it was synonymized with the subgenus *Haenydra* by Orchymont (1925), reinstated to a valid subgenus by Berthélemy (1986), included in *Hydraena* (sensu stricto) by Jäch (1988), treated as a valid subgenus by Hansen (1991), and again included in *Hydraena* (sensu stricto) by Jäch (1992*b*).

This taxonomic instability stems from misapplication of the fact that the type species of this taxon, *minutissima* Stephens (= *atricapillus* Waterhouse), and other species usually placed in *Hadrenya,* have the primitive elytral strial configuration, but lack any identifiable synapomorphies.

Following Jäch (1988, 1992*b*) and placing these species in *Hydraena* (sensu stricto) is not merely a technical mistake, it makes that taxon a polyphyletic one. This is because another currently recognized taxon, the subgenus *Phothydraena,* is phylogenetically more closely related to the remaining, more derived species of *Hydraena* (sensu stricto), than are any of the species placed in the subgenus *Hadrenya.*

Some hypomeral features of *H. minutissima, H. sharpi,* and *H. pygmaea* correlate with the basal-type elytral configuration. For example, similar to the condition found in the subgenus *Haenydra,* the end-apparatus of the exocrine glands emptying into the hsd-sulcus lie just below the pores (i.e., they have very short ductules), and the pores form a slightly irregular line. However, the opening of the antennal pocket and the distribution of the hap-setae is similar to the basal state of the various configurations present in *Hydraena* (sensu stricto; i.e., derived relative to *Haenydra*).

This combination of hypomeral and elytral characters supports a hypothesis of divergence from the lineage leading to *Hydraena* (sensu stricto) occuring early, after the divergence of the subgenus *Haenydra,* and before the divergence of the subgenus *Phothydraena* (see below).

For these reasons, *Hadrenya* is hereby reinstated as a valid subgenus. It should comprise species that have a strial configuration less than (3–)a(3–)b(3–)c (a–c being nervures, see Berthélemy, 1986, and Perkins, 1989), and lacking the divergent aedeagus (no parameres) and less derived antennal pocket/hap-setae configurations of *Haenydra.*

In addition to *minutissima* (the type species), *sharpi* and *pygmaea* are included in this subgenus. Placement of other species in *Hadrenya,* or transferral from *Hadrenya* to *Hydraena* (sensu stricto) should be based on study of transparency mounts and SEM.

Most systematists agree that generic level taxa should correspond to the criteria of monophyletic sister groups. If strong synapomorphies (especially ones ecologists can see!) are demonstrated, then generic-level taxa, instead of subgenera, should be used.

Subgenera, in my view, must necessarily meet a sufficient subset of these strict phylogenetic criteria. A subgenus should never (knowingly) be polyphyletic. Nor should a subgenus be paraphyletic in the sense of having relatively underived species lumped together (because of symplesiomorphy) with species that form a monophyletic group. However, having satisfied these criteria, a subgenus for species arising near the base of a lineage serves to highlight the need for additional study.

Subgenus *Phothydraena* Kuwert
(Fig. 10B; 16A, B; 18; 20A, B)

This taxon, represented by the type species *H. testacea,* has several features of the hypomeron that suggest a divergence after *Haenydra* and *Hadrenya,* and near the base of *Hydraena* (sensu stricto). This evidence is consistent with the "intermediate" strial configuration of *Phothydraena.*

The common ancestor of the *Hydraena* lineage, after the divergence of *Haenydra,* probably had the antennal pocket and hap-setae similar to that present in *H. riparia.* From this grade can be derived the two different forms: *Phothydraena* and the more derived forms of *Hydraena* (sensu stricto).

In *Hydraena* (sensu stricto), and more so in *Haenydra,* the secretion-spreading surface exists on each side of the hsd-sulcus. In other words, between the hsd-sulcus and the lateral extreme of the hydrofuge pubescence, the cuticle is smooth. Contrastingly, in *testacea* the hydrofuge is virtually contiguous with the hsd-sulcus, and the hypomeral carina is narrow and quite convex. This structural arrangement appears to be synapomorphic for *Phothydraena.*

The hap-setae of *testacea,* although arrayed adjacent to the antennal pocket, are not positioned on the anterior extreme of the hypomeral carina, as they are in *Hydraena* (sensu stricto). Their position appears more derivable from the configuration found in *riparia,* than from the condition where the hap-setae are present on the anterior extreme of the hypomeral carina, as in most *Hydraena* (sensu stricto).

These structures, plus the less derived (not tightly clustered) antennal cleaner, seem to support the current placement of *Phothydraena* based on the intermediate elytral strial configuration, and the synapomorphies discussed by Berthélemy (1986). Consequently, subgeneric status for *Phothydraena* is supported.

Subgenus *Hydraenopsis* Janssens, **new synonymy**

This taxon is based solely on the reduced condition of the parameres. Previously, I illustrated that paramere size and placement are highly variable, and synonymized *Hydraenopsis* with *Hydraena* (Perkins, 1981:62). Berthélemy (1986: 183) concurred with this placement, based on the fact that the type species of *Hydraenopsis* has 15 elytral striae, a derived condition, synapomorphic for *Hydraena* (sensu stricto). Nevertheless, Jäch (1986:22) raised *Hydraenopsis* to a distinct subgenus of *Hydraena*: "I believe that [*Hydraenopsis* forms] a monophyletic group which is quite difficult to define because most of the character states are plesiomorphic."

Clearly, the hypomeron of "*Hydraenopsis*" has the derived condition(s) described above. These derived states are shared with many temperate species of *Hydraena* (sensu stricto) that possess the plesiomorphic condition for the aedeagus: parameres inserting basally (e.g., *circulata* group). Are we to consider this group *Hydraenopsis*? This would make the two largest subgenera ill-defined and result in abundant uncertain and unsupportable species' placement, where distribution (European vs. non-European?) "defines" taxa. In contrast, the subgenus *Hydraena* (sensu stricto) that is based on the derived elytral strial configuration is both accurate and practical.

The fact that all of the elytral strial configurations of *Hydraena* are represented in the Palearctic fauna, and that species with intermediate strial configurations are found *only* in the Palearctic surely indicates that the maximum strial configuration of *Hydraena* (sensu stricto) evolved in Laurasia, and that tropical clades with this same configuration did not evolve that configuration in Gondwanaland. The hypomeral morphoclines correspond completely with those of the elytral stria duplications. *Hydraenopsis* is therefore reduced (again) to synonymy with *Hydraena.*

Subgenus *Spanglerina* Perkins, **new synonymy**

In an earlier paper (Perkins, 1989:455) I reduced *Spanglerina* Perkins, 1981, to a subgenus, and suggested that this status be used until the structures of *Hydraena* are more completely known. Study of transparency mounts reveals that the hypomeral structure of *Spanglerina* is similar to that of *Hydraena* (sensu stricto). *Spanglerina* is therefore hereby synonymized with *Hydraena.*

The hap-setae configuration in this group (properly termed the *ingens* species group), differs slightly from the usual for *Hydraena* (sensu stricto), as perhaps one might (now) expect, given the unusual microhabitat of species in this group: leaf packs trapped behind boulders in Neotropical streams (Perkins, 1981).

Genus *Adelphydraena* Perkins
(Fig. 52, 53)

The primitive features of the mouthparts, antennae, and elytra of the genus *Adelphydraena,* as well as the features synapomorphic with *Hydraena,* were described by Perkins (1989). The postocular, genal, and hypomeral features described below differ markedly from those of *Hydraena,* corroborating the separate generic status.

The postocular and genal areas (on each side of the antennal groove; Fig. 52A, B) are clothed in hydrofuge pubescence, but lack all of the derived cuticular features described above for *Hydraena* (i.e., peg sensilla, grooved sensilla, and genal antennal pocket setae). Derived genal features unique to *Adelphydraena* include a bottle-shaped sensillum (Fig. 53B:l) located in a shallow depression medial to the antennal groove, and three very long flagelliform setae (Fig. 53B: g) located on the medial margin of the shallow depression.

Unlike *Hydraena* the antennal pocket does not open ventrally, the ventral margin being closed by the hypomeron, which bears two setae (Fig. 52:b). An antennal cleaner is not present, the medial margin of the antennal pocket having only a few simple setae (Fig. 53:f).

The hydrofuge pubescent part of the hypomeron is shaped differently than that of *Hydraena,* being lobe-shaped in the anterior part (Fig. 52C, D). In this lobe-shaped part are many hemispherical "globules"—presumed exocrine secretions (Fig. 52D:s). Also present in this area are relatively large setae that appear to be basiconic (Fig. 52D:h). When treated with strong potassium hydroxide, the hydrofuge setae remain, but the presumed basiconic sensilla are removed (Fig. 53C:r).

Although a distinct hypomeral carina is present, no hypomeral exocrine secretion groove was found. However, additional study is needed to determine the distributions of exocrine glands associated with the hypomeron.

Unique to this genus is a chemosensory/secretory fovea located laterally on the fifth abdominal sternum (Fig. 53E:x). The fovea, present in both sexes, has basiconic sensilla (Fig. 53F:t) and what appear to be secretion globules. In common with *Hydraena,* the last sternum of females has a pair of sensory clusters (Fig. 53E:y).

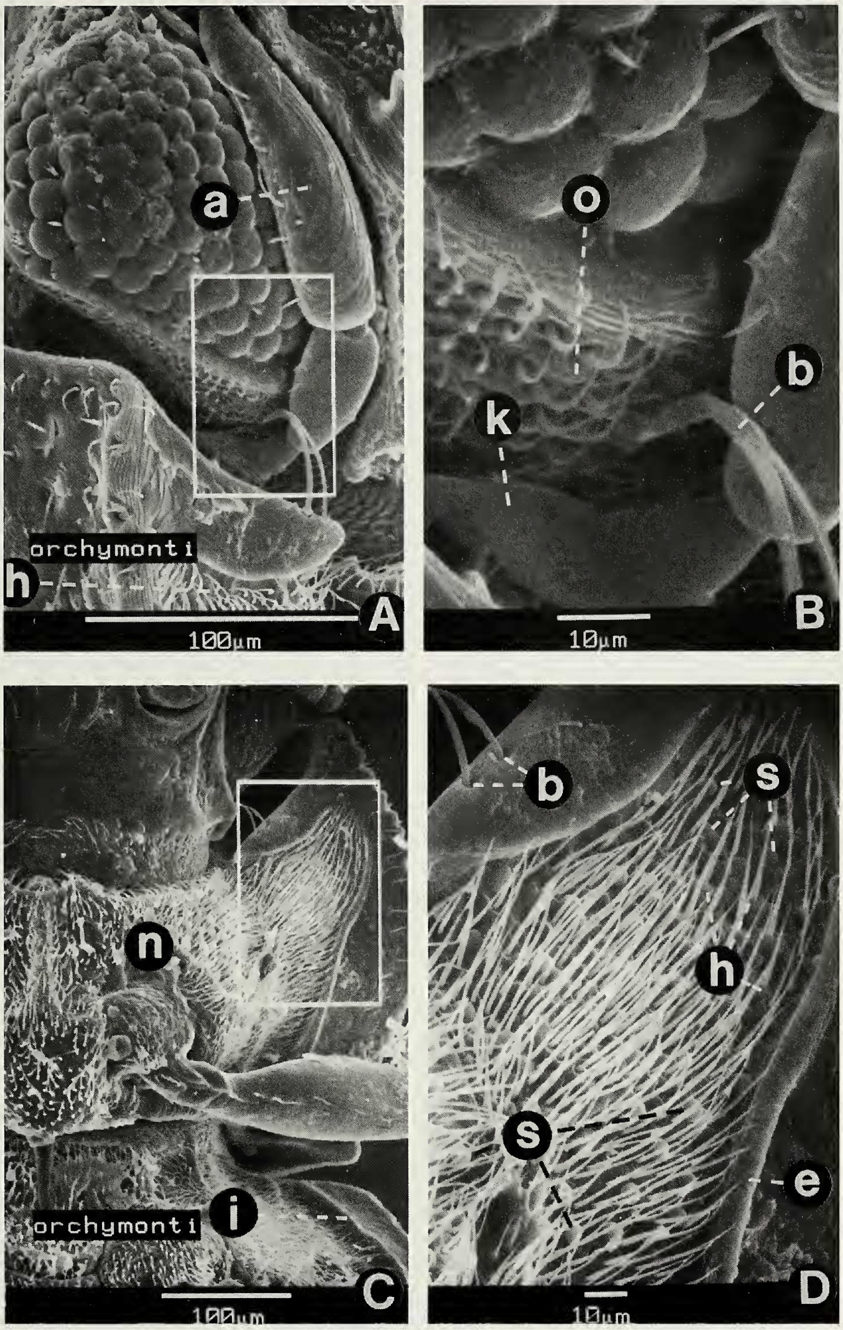


Fig. 52.—*Adephydraena orchymonti.* A. Eye and prothorax, lateral aspect of right side. B. Rectangular area of A, enlarged. C. Prothorax, ventral aspect of left side. D. Rectangular area of C, enlarged. Structures: (a) first antennomere, (b) marginal setae of antennal pocket, (e) hypomeral carina, (h) hydrofuge setae and basiconic sensilla, (i) carina of elytral epipleuron, (k) cupule article of antenna, (n) prosternum, (o) postocular hydrofuge, (s) presumed exocrine secretion.

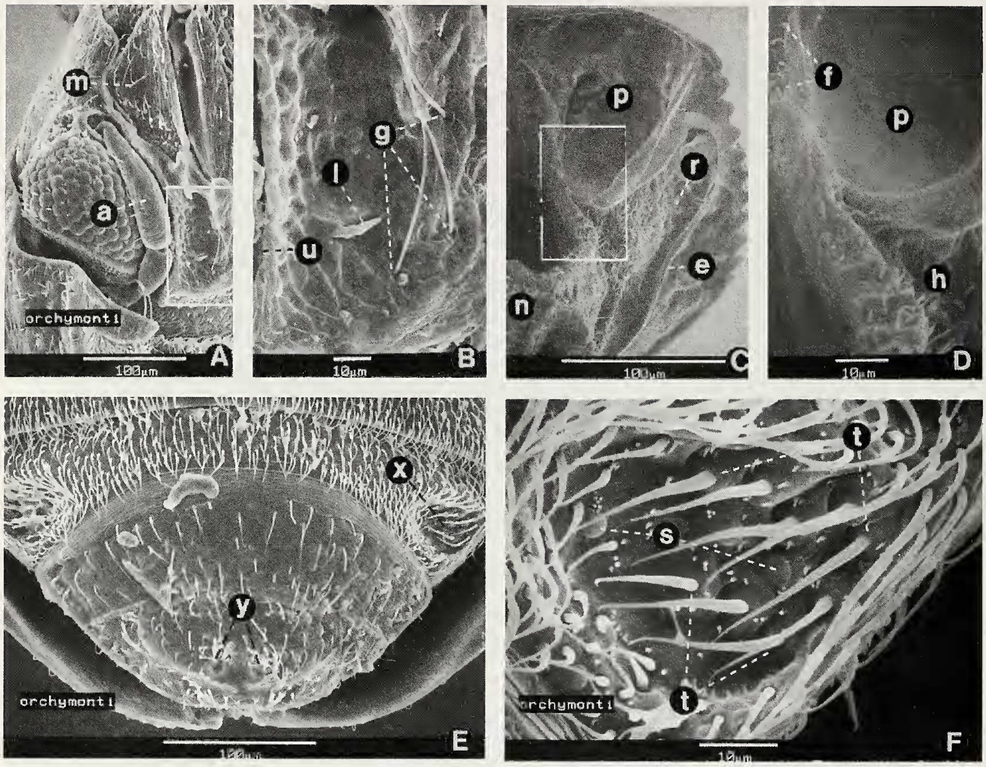


Fig. 53.—*Adephydraena orchymonti.* A. Head and anterior part of prothorax, lateral aspect of right side. B. Rectangular area of A, enlarged. C. Prothorax (treated with hydroxide), ventral aspect of left side. D. Rectangular area of C, enlarged. E. Abdominal apex, ventral aspect. F. Sensory fovea of abdomen. Structures: (a) first antennomere, (e) hypomeral carina, (f) setae on medial margin of antennal pocket, (g) genal setae, (h) hydrofuge of hypomeron, (l) bottle-shaped sensillum, (m) mandible, (n) prosternum, (p) antennal pocket, (r) sockets of hypomeral basiconic sensilla, (s) presumed exocrine secretion, (t) sensory setae, (u) subocular antennal groove, (x) sensory fovea of abdomen, (y) sensory clusters of last abdominal sternum.

Tribe Hydraenidini Perkins

This tribe comprises the three South American genera *Hydraenida, Parhydraenida,* and *Haptaenida.* Although many of the characters that diagnose members of this tribe are probably plesiomorphic, the species have a general external similarity, and have the two presumed synapomorphic characters given below.

Members have the following hypomeral features (numbers 3 and 4 probably apomorphic): (1) the antennal pocket is located in the anterior face of the hypomeron, at least partially closed ventrally by the anterior extreme of the hypomeron; (2) the setae on the anteroventral margin of the antennal pocket are very small, not pocket-forming; (3) the nonmarginal setae on the anterior part of the wet-hypomeron are long and flexible; and (4) the hypomeral carina is contiguous (or nearly so) with the notosternal suture, hence the hydrofuge pubescence is restricted to the postcoxal pronotal projection (Fig. 54A, B).

Retained plesiomorphic features of the Hydraenidini include the following: (1) the antenna has 11 articles (six + club), (2) the postocular area lacks specialized

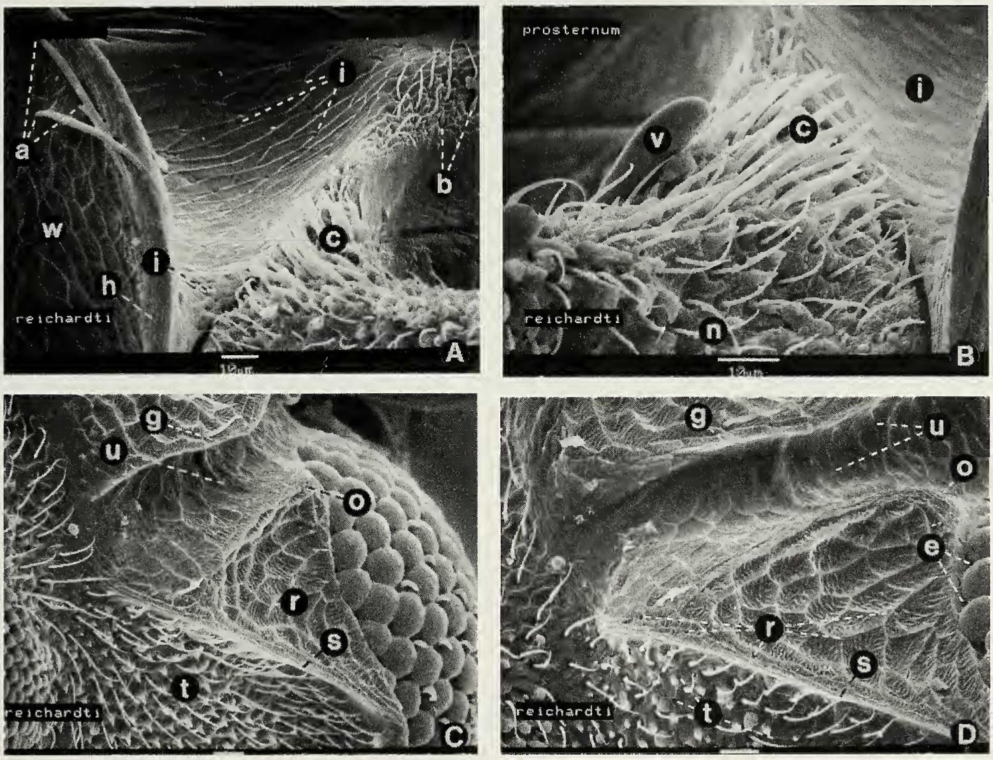


Fig. 54.—*Parhydraenida reichardti.* A. Antennal pocket area of prothorax, right side. B. Prosternum. C. Eye and subocular area, posteroventral aspect. D. Subocular area, ventrolateral aspect. Structures: (a) hypomeral flexible setae, (b) bottle-shaped sensilla, (c) antennal cleaner of prosternum, (e) periocular pores, (g) genal ridge of subocular antennal groove, (h) hypomeral carina, (i) antennal pocket and exocrine pores, (n) prosternum, (o) exocrine pore cluster, (r) postocular triangular reticulate area and exocrine pores, (s) postocular ridge, (t) postocular asperite hydrofuge and exocrine pores, (u) subocular antennal groove and exocrine pores, (v) cervical sclerite, (w) wet-hypomeron.

sensilla, and (3) the pronotum has single (nonpaired) punctation. The last sternum, in both sexes, is largely exposed and bears setae.

Genus *Parhydraenida* Balfour-Browne
(Fig. 54)

Discussion.—The genus *Parhydraenida,* currently comprising nine species from southeastern Brazil and Ecuador, is comparatively uniform in external morphology among the species. The following description is based on SEM preparations of *P. reichardti* and transparency mounts of *P. bubrunipes.*

Description.—**Antennal pocket.** Periocular exocrine pores (Fig. 54:e) are present at the posterior margin of the eye. The subocular antennal groove (Fig. 54:u) is deep, its medial margin cariniform, forming a distinct channel. A postocular triangular reticulate area (Fig. 54:r) is located at the posteroventral angle of the eye. This triangular area lacks hydrofuge pubescence and has exocrine pores at the intersects of some of the microreticulations (Fig. 54:r), and a small cluster of pores (e.g., ca. ten in *P. bubrunipes*) at the anterior angle of the triangular area (Fig. 54:o). A sharp postocular carina (Fig. 54:s) forms the posterior rim of the triangular reticulate area, and separates the latter from the postocular asperite hydrofuge (Fig. 54:t). The postocular area lacks any specialized exocrine secretion delivery setae or sensilla.

A well-developed, rounded hypomeral carina (Fig. 54:h) separates the wet- and much smaller bubble-hypomeron. Anteriorly, the hypomeral carina is contiguous (or nearly so) with the notosternal suture, hence the hydrofuge pubescence of the bubble-hypomeron is entirely (or nearly so) restricted to the notal postcoxal projection.

The wet-hypomeron (Fig. 54:w) is wide, microreticulate, and has random exocrine pores at some of the intersects of the microreticulation. In one species, *P. bubrunipes,* these pores are extremely dense over the lateral three-fourths of the wet-hypomeron, but absent over the medial fourth (including near the carina). There are neither organized clusters of pores, nor a secretion sulcus on the hypomeron.

Near the anterior extreme of the wet-hypomeron, set back from the margin, are six to eight elongate hypomeral flexible setae (Fig. 54:a). These setae are flexible in their sockets, and are not rigid enough, nor appropriately placed, to form part of the antennal pocket. Present on the anterior margin of the antennal pocket, but not large enough to form part of the antennal pocket, are a few very small setae, about five in number.

The antennal pocket (Fig. 54:i) is deep, lacking hydrofuge pubescence, the surface microreticulate and having randomly distributed, moderately dense exocrine pores. The pores are more concentrated at the posterior extreme of the antennal pocket. Medial to the antennal pocket, the notal area is asperite hydrofuge and has two bottle-shaped sensilla (Fig. 54:b).

A dense cluster of sharp spines and stiff setae, the prosternal antennal cleaner (Fig. 54:c) is located at the anterolateral angle of the prosternum. Some of the setae in this spine cluster appear to be shallowly grooved; it is possible that some are chemoreceptors. The antennal cleaner is surrounded by asperite hydrofuge.

Genus *Hydraenida* Germain

Discussion.—The genus *Hydraenida* currently comprises two species from Chile, *H. ocellata* and *H. robusta.* The following description is based on transparency mounts of both of these species.

Description.—**Antennal pocket.** The distinctive reticulate, triangular postocular area of *Parhydraenida* is absent in *Hydraenida,* the corresponding area with smooth cuticle and lacking a ridge. However, exocrine pores are found in corresponding locations in the two genera: in *Hydraenida* a tight cluster of about 12 pores is present in the location corresponding to the ridge-mounted exocrine pore cluster of *Parhydraenida* (Fig. 54C:o), and a separate group of pores, about 12, is present in the area corresponding to the reticulate triangular area of *Parhydraenida* (Fig. 54C:r). The postocular carina is present in both genera (Fig. 54C:s).

The hypomeron differs from that of *Parhydraenida* as follows: (1) a narrow, smooth, and nonhydrofuge pubescent gap exists between the hypomeral carina and the notosternal suture (these structures being contiguous in *Parhydraenida*); (2) the margin of the hypomeron at the antennal pocket is less arcuate; (3) the prominent, flexible, and loosely socketed setae near the anterior margin of the hypomeron of *Parhydraenida* (Fig. 54A:a) are apparently absent (more specimens of *Hydraenida* are needed to confirm this); (4) the smooth area between the hypomeral carina and the hydrofuge of the postcoxal projection is slightly wider in *Hydraenida*; and (5) the posterior area of the hypomeron is wider in *Hydraenida,* correlated with the nonsinuate posterior sides of the prothorax. Apparently the prosternum of *Hydraenida* lacks the antennal cleaning cluster of spines present in *Parhydraenida* (Fig. 54B:c). However, more specimens and SEM study are needed to confirm this.

Haptaenida, new genus

Type Species.—Haptaenida huggerti, new species.

Diagnosis.—Recognized by the laterally open antennal pockets (Fig. 55), the 11 articles of the antenna (six + club), the ocelli located closer to the midline than to the eyes, the moderately short maxillary palpi with length ratios of last three articles as six : three : seven, the transverse, noncordiform pronotum with anterior and posterior hyaline margins, the posteriorly narrowed and transversely convex elytra, the restricted abdominal hydrofuge pubescence, the very large wet-hypomeron, and the features of the postocular/hypomeral antennal pocket (see morphological section).

Description.—**Antennal pocket.** The postocular area and the hypomeron of *Haptaenida huggerti,*

n. gen., n. sp. (formally described in a following section) differ from *Parhydraenida* in the following respects (no slide mounts studied). In the postocular area, the region corresponding to the distinctive reticulate triangular area of *Parhydraenida* (Fig. 54C:r) is shining and shaped differently in *Haptaenida,* being more elongate and medially arcuate. The antennal subocular sulcus is wider in *Haptaenida* than in *Parhydraenida.* The postocular carina is present in both genera (Fig. 54C:s).

The hypomeron has the ventral opening to the antennal pocket wider than in *Parhydraenida.* The prominent, flexible, and loosely socketed setae near the anterior margin of the hypomeron of *Parhydraenida* (Fig. 54A:a) are apparently absent (more specimens are needed to confirm this). In addition to these differences, the antennal pocket is open in lateral aspect in *Haptaenida* (Fig. 55), and closed in *Parhydraenida.* Apparently the prosternum of *Haptaenida* lacks the antennal cleaning spines present in *Parhydraenida* (Fig. 54B:c). However, more specimens and SEM study are needed to confirm this.

Other characters. Body size moderate, form elongate oval and posteriorly narrowed, weakly convex, elytra more strongly so, head not deflexed. Antennomeres 11 (six + club), third slightly longer than combined lengths of fourth to sixth. Maxillary palpi moderately long, length ratios of articles two to four (last) as six : three : seven. Eyes rather small, not elevated. Gena with low transverse ridge behind cardo. Labrum moderately large, not set at angle to clypeus, apicomedially emarginate; anterior margin fringed with setae. Clypeus anterior margin straight. Ocelli small and weakly convex, each located twice as far from eye as from midline, frons not convex between ocelli; area behind and between ocelli lacking carinae. Pronotum with anterior transverse fovea broadly joined to lateral depressions; a short, shallow transverse fovea behind midlength; sides from midlength to anterior angles straight and slightly convergent, from midlength to posterior angles more strongly convergent and slightly concavely arcuate. Anterior hyaline border narrow, present in weak emargination over median half of anterior margin. Posterior hyaline border very narrow. Elytra with weak rows of punctures, becoming more irregular laterally. Antennal pocket large, shining, open ventrally and laterally. Prosternum in front of procoxae shorter than procoxal cavities, latter open behind. Metasternum reduced, shorter than mesosternum, with shallow midlongitudinal impression. Intercoxal sternite small, triangular. Legs and tarsi short, tarsi apparently five–five–five (no slide mount). Both sexes with abdominal sterna one to four about equal in length, fifth slightly longer than fourth; seventh visible beyond posterior margin of sixth; first and lateral thirds of second hydrofuge pubescent, remainder with sparse, more robust setae. Hydrofuge pubescence also present on postocular area, bubble-hypomeron (except antennal pockets), notal postcoxal projections, mesosternum, and metasternum. Wingless.

Etymology.—Greek, *hapt* (join, lay hold of) plus *aenida* (from *Hydraenida*), in reference to the unusual aedeagus and flightlessness; gender feminine.

Haptaenida huggerti, new species
(Fig. 55, 56)

Type Material.—Holotype male and one paratype of each sex: Ecuador, Napo, Quito–Baeza road, 4,100 m, iii.1983, leg. Huggert and Masner; deposited in MCZ.

Description.—Size (mm × 100; length/width): body 224/89, head 42/60, pronotum 51/80, elytra 128/89. Dorsum black to dark brown, with inconspicuous setae; legs and maxillary palpi brown. Labrum and clypeus dull, micropunctulate. Frons shallowly, densely punctate, dull. Labroclypeal suture shallow. Shallow, densely micropunctulate depression between eye and ocellus. Pronotal disc moderately densely, shallowly punctate, interstices shining, 0.5–2.0 times puncture diameter, becoming more densely punctate laterally. Elytra with ten slightly irregular series of shallow punctures, each puncture with a fine, short, granule-based seta; intervals with similar granule-based setae, slightly denser on intervals four, six, and eight, interval eight slightly raised. Last abdominal sternum, in male, apically truncate; in female strongly arcuate. Last tergum, in male, apically truncate and with a patch of setae on each side; in female weakly arcuate and with shorter setae than in male. Aedeagus (Fig. 56) lacking parameres and with two large distal processes; length 0.51 mm.

Etymology.—Named in honor of Lars Huggert, who collected the specimens.

Discussion.—Anders Nilsson kindly provided the following information on the type locality: "The specimens were collected in a small lake (ca. 10 × 10 m) on open ground. Most of the area was peaty with scattered elfin forest, but the lake was surrounded by mineral (morainic) ground. The beetles were collected at the lake margin among stones and silt. There was almost no vegetation in the lake and some low grasses on the surrounding ground. It was very windy, with eastern winds prevailing, from the Amazonas."

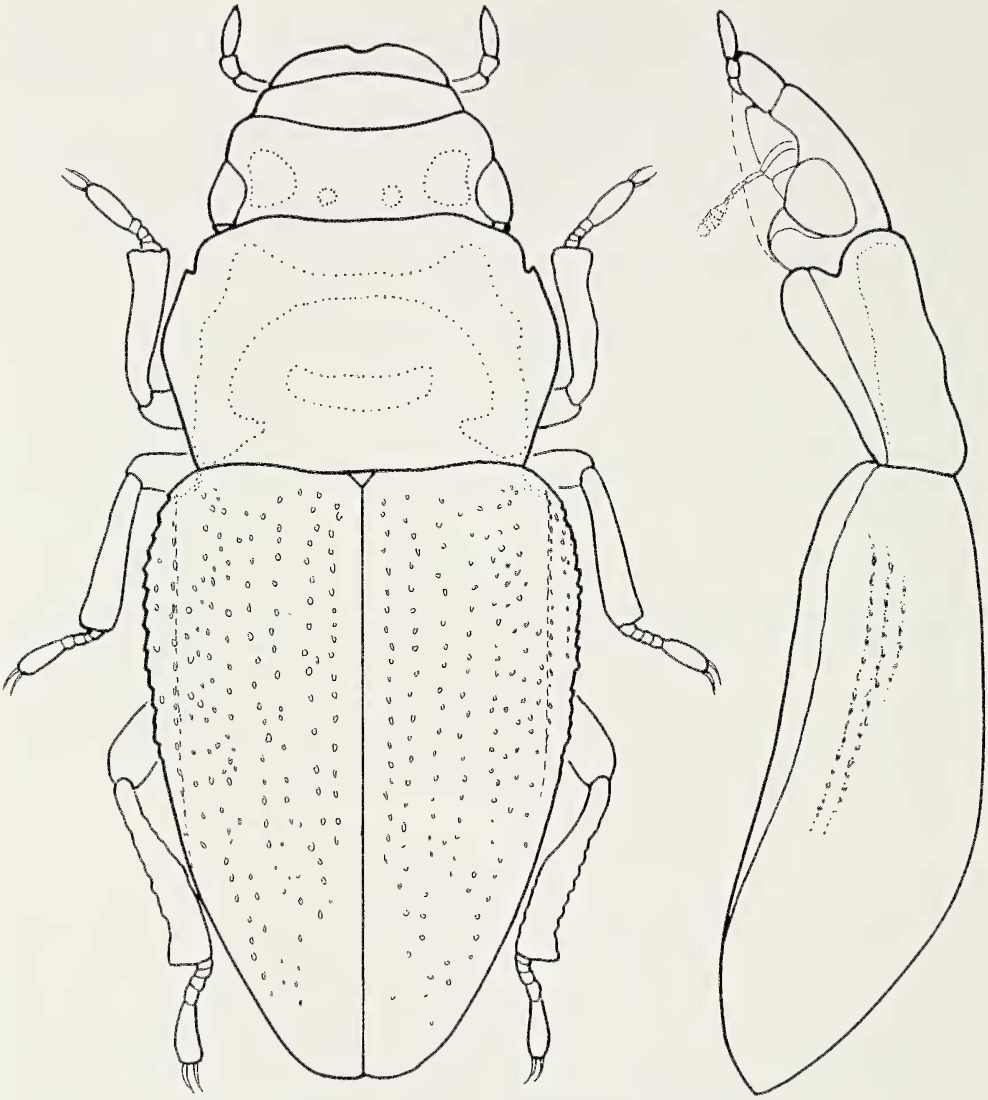


Fig. 55.—*Haptaenida huggerti*, dorsal and lateral aspects.

Parhydraenini, **new tribe**

This tribe comprises the genera *Pneuminion* n. gen., *Parhydraena, Protozantaena* n. gen., and *Discozantaena.* Members of the tribe are characterized by the following presumed synapomorphic characters: (1) the antennal pocket is formed by stiff, arcuate hypomeral setae the most medial of which emerge from the anterior extreme of the hypomeral hydrofuge (secondarily reduced in *Discozantaena*); (2) the prosternum has a cluster of specialized spines on each side (“zantes” = presumed antennal cleaner); and (3) the pronotum has distinctive “paired” punctation.

Additional diagnostic features, presumably plesiomorphic include: (1) the post-

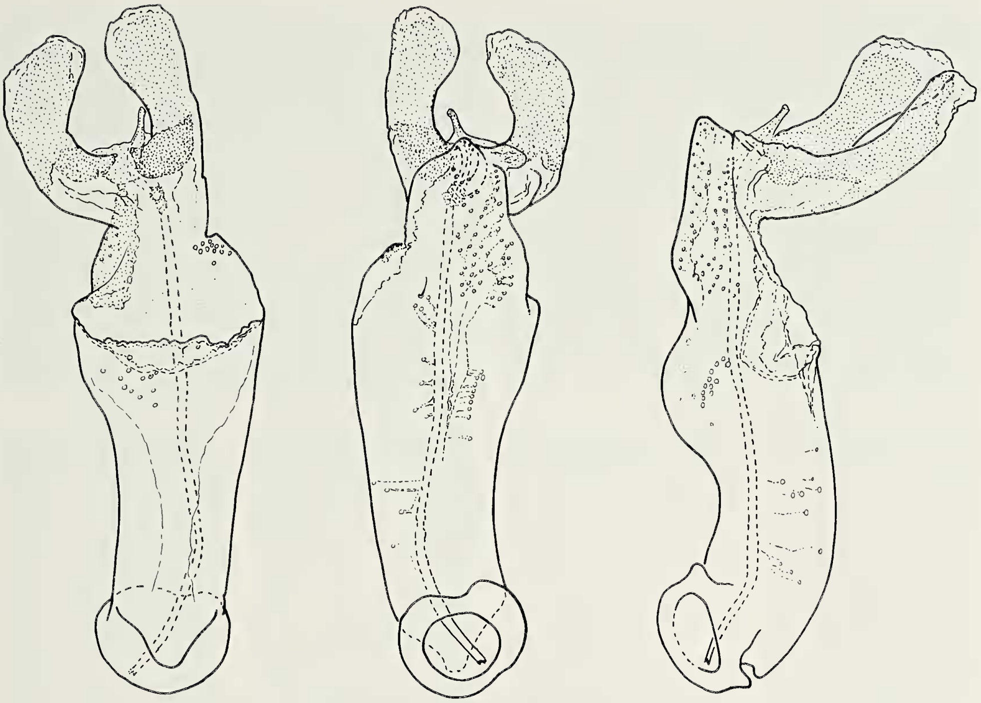


Fig. 56.—*Haptaenida huggerti*, aedeagus of holotype.

ocular area lacks specialized sensilla, (2) the hypomeral hydrofuge attains the antennal pocket, and (3) the wet-hypomeron lacks elongate and flexible setae.

The genera *Protozantaena* and *Discozantaena* share an unusual derived aedeagus having a characteristic shape, long terminal flagellum, and very short parameres. The genus *Pneuminion* can be considered to have branched off early in this clade, based on the retained ancestral condition of 11 antennomeres (the three other genera having ten antennomeres). This early divergence is also suggested by the "reversed" architecture of the antennal pocket—open dorsally via postocular emargination of the pronotum, and closed ventrally by the anterior part of the wet-hypomeron.

Pneuminion, new genus

Type Species.—*Pneuminion velamen*, new species.

Diagnosis.—Recognized by the 11 articles of the antenna (six + club), the ocelli located midway between the midline and the eyes, the moderately short maxillary palpi with length ratios of last three articles as five:four:eight, the transverse, noncordiform pronotum lacking hyaline margins and with well-developed postocular emarginations, the elytra with ten very regular series of very shallow punctures and all interseries equally developed, the restricted abdominal hydrofuge pubescence, the very large wet-hypomeron, and the features of the postocular/hypomeral antennal pocket (see morphological section).

Description.—**Antennal pocket.** The hypomeral carina is well defined, angulate posteriorly, and becomes obsolete anteriorly at the antennal pocket. The bubble-hypomeron is narrow and very sparsely pubescent opposite the notosternal suture.

The wet-hypomeron is very wide, slightly wider anteriorly than posteriorly, reticulate, nonsetose (except hap-setae), and with very sparse, randomly distributed exocrine pores. A row of 12–15 well-developed hypomeral antennal pocket setae are located along the ventral margin of the antennal pocket; these setae are closely spaced, each widest in the middle, tapering apically, and flattened. The setae become progressively longer from the most lateral to the most medial, the latter arising from the anterior extreme of the hydrofuge hypomeron, adjacent to the lateral extreme of the procoxal cavity. There are no organized clusters of exocrine pores or end-apparatus, and no secretion sulcus exists on the hypomeron.

The antennal pocket is located in the anterior face of the prothorax, moderately deep, opened ventromedially (between the hap-setae and the prosternum) and dorsally (at the postocular emarginations); the middle portion of the pocket is convex, partially dividing the pocket into a dorsal and a ventral concavity. About nine exocrine pores are located along the medial margin of the pocket, next to the notosternal suture; otherwise the pocket has very few, randomly distributed exocrine pores.

A dense cluster of sharp spines, the prosternal antennal cleaner is located on the anterolateral margin of the prosternum. The antennal cleaner is surrounded by sparsely pubescent asperite hydrofuge.

Periocular exocrine pores are present along the subocular antennal groove and at the posterior margin of the eye. The medial margin of the antennal groove is raised slightly, not cariniform. A few exocrine pores are located near the posteroventral angle of the eye. A well-developed postocular ridge delimits the postocular and subocular areas. The postocular area is clothed in hydrofuge pubescence, but lacks any specialized exocrine secretion delivery setae or sensilla.

Other characters. Body size moderate to small, form elongate oval, moderately convex dorsally, head not deflexed. Antennomeres 11 (six + club), third slightly longer than combined lengths of fourth to sixth. Maxillary palpi moderately short, length ratios of articles two to four (last) as five:four:eight. Eyes well developed, not elevated. Labrum large, set at angle to clypeus, apicomedially deeply incised; anterior margin fringed with long setae. Clypeus anterior margin straight. Ocelli located midway between midline and eyes, frons very weakly convex between ocelli; area behind and between ocelli lacking carinae. Pronotum with anterior midlongitudinal fovea, behind which is a U-shaped fovea; lateral depressions not demarked by foveae; lateral margin arcuate. Hyaline borders absent; setal fringe on base in front of scutellum. Elytra with ten rows of punctures. Antennal pocket as described in morphology section. Prosternum in front of procoxae shorter than procoxal cavities, latter open behind. Metasternum with shallow midlongitudinal impression. Intercoxal sternite small, triangular. Legs moderately elongate, tarsi five–five–five. Abdominal sterna one to four about equal in length, fifth slightly longer than fourth; in male, seventh concealed beneath sixth; in female seventh visible beyond posterior margin of sixth; first and basal part of second hydrofuge pubescent, remainder with sparse, fine, long setae. Hydrofuge pubescence also present on postocular area, bubble-hypomeron (except antennal pockets), notal postcoxal projections, mesosternum, and metasternum.

Etymology.—Greek, *pneum* (breathe) plus *inion* (nape of the neck), in reference to the pronotal postocular emarginations of the antennal pocket; gender neuter.

Pneuminion velamen, new species

Type Material.—Holotype male and 25 paratypes: South Africa, Cape Province, Cederberg, 1130 m, sifted marsh shore, 32.28S–19.14E, 7.xi.1983, Endrody-Younga (#2055); deposited in TMSA. Additional paratypes: Cape Province, Farm Ezelsfontein, shorewashing, 30.24S–18.05E, 30.x.1977, Endrody-Younga (#1407); (4 TMSA). S. W. Cape, Hawaquas rad. tower, 33.41S–19.06E, shore washing, 27.X.1978, Endrody-Younga (#1484); (5 TMSA). Cape-Swartberg, Seweweekspoort Klf, 33.24S–21.21E, river stones, 18-XI-1973, Endrody-Younga (#269); (1 TMSA). W. Cape, Hawequas, 33.34S–19.08E, from rock pools, 6.XI.1973, Endrody-Younga (#210); (3 TMSA). S. W. Cape, Limiet Berge, 33.33S–19.07E, water collection at 950 m, 7.XI.1973, Endrody-Younga (#215); (1 TMSA). Cape, Cederberg, Eikenboom, 900m, 32.27S–19.10E, river stones, 29-X-1981, Endrody-Younga (#1906); (2 TMSA). Representative duplicate specimens deposited in MCZ and CMNH.

Description.—Size (mm × 100; length/width): body (length to elytral apices) 191/84, head 36/51,

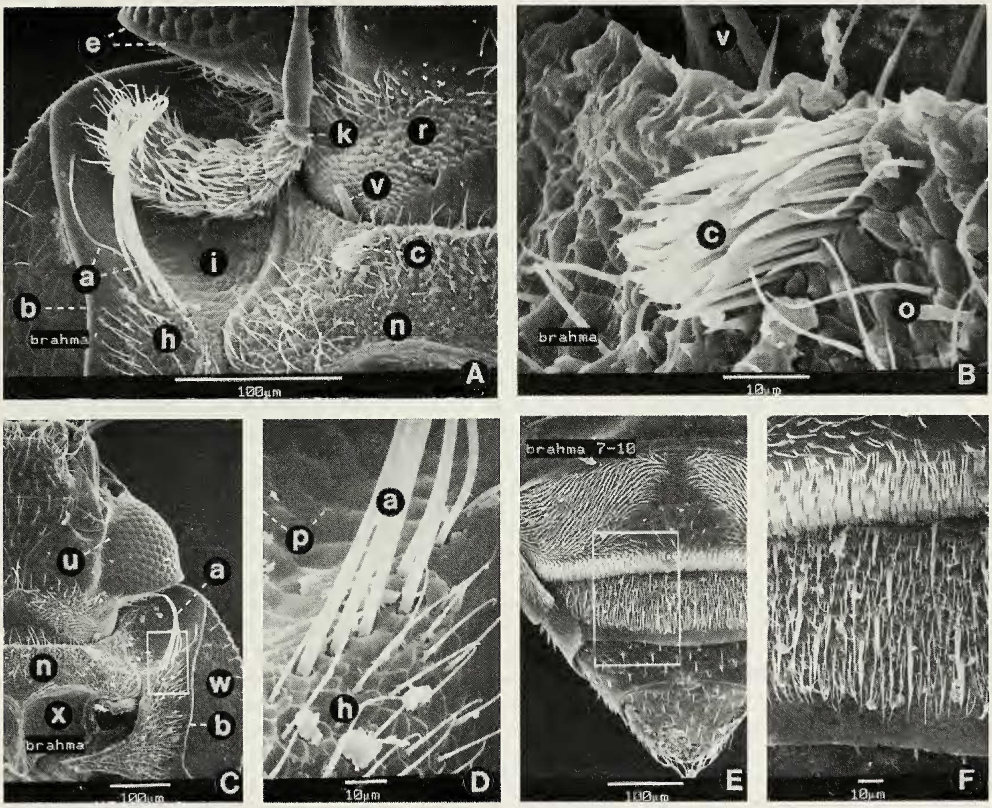


Fig. 57.—*Parhydraena* (undescribed species "BRA," from South Africa). A. Antennal pocket and associated structures, right side. B. Antennal cleaner of prosternum. C. Head and prothorax, ventral aspect of left side. D. Rectangular area of C, enlarged. E. Abdominal terga 7–10. F. Rectangular area of E, enlarged. Structures: (a) hypomeral antennal pocket setae, (b) hypomeral carina, (c) antennal cleaner of prosternum, (e) eye and periocular exocrine pores, (h) hypomeral reticulate hydrofuge, (i) antennal pocket, (k) cupule article of antenna, (n) prosternum, (o) prosternal asperite hydrofuge, (p) exocrine pores of antennal pocket, (r) genal asperite hydrofuge, (u) subocular antennal groove, (v) cervical sclerite, (w) wet-hypomeron, (x) procoxa.

pronotum 42/69, elytra 119/84. Dorsum black, with moderately dense, conspicuous white setae; legs and maxillary palpi brown. Labrum, clypeus, and frons dull, micropunctulate. Labroclypeal suture shallow. Shallow fovea in front of each ocellus. Pronotal postocular emarginations deeper and less symmetrical in females than in males. Pronotum dull, entirely micropunctulate, subrugose; oblique anterior fovea on each side shallowly connecting to midlongitudinal fovea; posterior U-shaped fovea well developed; setae at lateral margin flat on cuticle in dry specimens. Elytra with setae of series and interseries equally developed, resulting in very discrete, narrowly separated, unilinear rows of setae, about 18 on each elytron, each seta granule-based; serial punctures very shallow (but internal columellae well developed); interseries very slightly raised; explanate margin narrow in both sexes.

Etymology.—Latin, *velamen* (robe, garment), in reference to the distinctive dorsal pubescence.

Discussion.—A figure of the male genitalia of *P. velamen,* and descriptions of additional new species in the genus will be given in a separate paper.

Genus *Parhydraena* Orchymont
(Fig. 57)

Discussion.—The characters described below are quite similar in all of the species of *Parhydraena* studied (see Appendix 1), including the type species *P.*

brevipalpis. The number of hap-setae varies from seven to 14. Their location relative to the hypomeral carina varies slightly, correlating with the width of the hypomeron, but their position relative to the prosternal antennal cleaner and head is more constant.

Parhydraena cooperi Orchymont, the type species of the subgenus *Pseudhydraena* Orchymont, has characteristics like those described below (12 hap-setae). The aedeagus of *P.* (*Pseudhydraena*) *cooperi* lacks parameres, and this seems to be the only distinction indicating, perhaps, a valid subgeneric status for *Pseudhydraena.*

Description.—**Antennal pocket.** A sharp, step-like hypomeral carina (Fig. 57:b) separates the wet- and bubble-hypomeron. Between the carina and the reticulate hydrofuge the cuticle is completely smooth, and has about 15 randomly spaced exocrine pores distributed along its length. There are no organized clusters of pores or end-apparatus, and no secretion sulcus exists on the hypomeron.

A cluster of well-developed antennal pocket setae (Fig. 57:a) are located at the posterior margin of the antennal pocket. These setae arise from the anterior extreme of the hydrofuge hypomeron, not from the anterior extreme of the wet-hypomeron as in *Hydraena.*

The antennal pocket (Fig. 57:i) is relatively wide and only moderately deep, lacking hydrofuge pubescence, the surface grading from smooth laterally to microreticulate medially. Within the pocket are randomly distributed exocrine pores (Fig. 57:p).

A dense cluster of sharp spines, the prosternal antennal cleaner (Fig. 57:c) is located near the anterior margin of the prosternum. This spine cluster is interpreted as an antennal cleaner based on its location and the orientation of the spines. The antennal cleaner is surrounded by asperite hydrofuge (Fig. 57: o), except the area between the cleaner and the antennal pocket, which is sharply asperite but lacks hydrofuge hairs—hence the movement of the antenna against the cleaner (when the antenna is raised during air capture) would not be impeded by hydrofuge hairs.

Periocular exocrine pores (Fig. 57:e) are present at the posterior margin of the eye and along the subocular antennal groove (Fig. 57:u). The postocular area is clothed in hydrofuge pubescence, but lacks any specialized exocrine secretion delivery setae or sensilla.

Genus *Decarthrocerus* Orchymont, **new synonymy**

Decarthrocerus jeanneli Orchymont, the type species of the genus, is similar in characteristics to those described above for *Parhydraena.* It differs in having six or seven hap-setae, only one or two fewer than the minimal number for known *Parhydraena.* This species also has a more deflexed labrum, but this is not of generic significance.

However, like *Parhydraena* (*Pseudhydraena*), the aedeagus of *D. jeanneli* lacks parameres. Therefore, *Decarthrocerus* is hereby synonymized with *Pseudhydraena* Orchymont (also described in 1948, but before *Decarthrocerus*; see Hansen, 1991, for literature citations).

Protozantaena, **new genus**

Type Species.—Protozantaena labrata, new species.

Diagnosis.—Recognized by the small size; the ten-articled antenna (five + club); the lack of an hypomeral carina; the weakly developed ocelli located midway between the midline and the eyes; the large maxillary palpi, as long as the antennae; apical article wide; inner surface arcuate at base; length ratios of last three articles as six:four:nine; the transverse, slightly cordiform pronotum with anterior hyaline margin and lacking postocular emarginations; the female abdominal apex; the male genitalia; and the features of the postocular/hypomeral antennal pocket (see morphological section).

Description.—**Antennal pocket.** The hydrofuge hypomeron is narrow adjacent to the procoxal cavity; lateral to the hydrofuge the hypomeron is smooth, slightly convex (noncariniform), and has sparse, random exocrine pores, about 16–20 along its length. The remainder of the wet-hypomeron is very weakly microreticulate. There are no organized clusters of pores or end-apparatus, and no secretion sulcus exists on the hypomeron. A row of 12–15 well-developed antennal pocket setae are located along the ventral margin of the antennal pocket. These setae are closely spaced, each widest in the middle, tapering apically, and flattened. The setae are progressively longer medially, the most medial arising from the anterior extreme of the hydrofuge hypomeron, adjacent to the lateral extreme of the procoxal cavity.

The antennal pocket is relatively wide and only moderately deep, not closed ventrally (except by pocket setae), lacks hydrofuge pubescence except at anteromedial extreme; a narrow band of minute spicules (in rows) is present along the medial margin. Within the pocket are randomly distributed exocrine pores.

A dense cluster of sharp spines, the prosternal antennal cleaner is located on the anterolateral margin of the prosternum. The antennal cleaner is surrounded by sparsely pubescent asperite hydrofuge.

Periocular exocrine pores are present along the subocular antennal groove and at the posterior margin of the eye. A few exocrine pores are located near the posteroventral angle of the eye. A well-developed postocular ridge delimits the postocular and subocular areas. The postocular area is clothed in hydrofuge pubescence, but lacks any specialized exocrine secretion delivery setae or sensilla.

Other characters. Body size small, form elongate oval, moderately transversely convex dorsally, head not deflexed. Antennomeres ten (five + club), second slightly longer than combined lengths of third to fifth. Maxillary palpus relatively large, as long as antenna, length ratios of articles two to four (last) as six:four:nine, apical article relative wide, inner surface arcuate basally. Eyes well developed, not elevated. Labrum large, rectangular, set at angle to and longer than clypeus, anterior margin nearly straight, fringed with long setae. Clypeus anterior margin and frontoclypeal suture very slightly arcuate. Ocelli weakly convex, located midway between midline and eyes, frons very weakly convex between ocelli; area behind and between ocelli lacking carinae. Pronotum with very indistinct, widely U-shaped fovea behind middle on disc; no foveae demarking lateral depressions; lateral margins sinuate behind midlength; anterior hyaline border present over median third, extremely narrow. Elytra with ten rows of punctures. Antennal pocket as described in morphology section. Prosternum in front of procoxae shorter than procoxal cavities, latter open behind; zantes present. Hypomeron lacking carina at margin of hydrofuge pubescence. Metasternum with shallow impression on disc in basal half. Intercoxal sternite small, triangular. Legs moderately elongate, tarsi five–five–five. Hydrofuge pubescence present on postocular area, bubble-hypomeron (except antennal pockets), notal postcoxal projections, mesosternum, metasternum, first four abdominal sterna, and basal part of fifth.

Etymology.—Greek, *proto* (first) plus *zantaena* (from *Discozantaena*); gender feminine.

Protozantaena labrata, new species
(Fig. 58C)

Type Material.—Holotype male: Namibia: Naukluft, Naukluft Park, 24.16S–16.15E, shore washing, 26.x.1974, Endrody-Younga (#431); deposited in the TMSA. Paratypes: same data as holotype, (95 TMSA); same locality, water collection, (#430), (1 TMSA); same locality, river stones, 23.viii.1982, (#1921), (3 TMSA); same locality, shore washing, river, 10.viii.1989, Endrody-Younga and Klim. (#2644), (432 TMSA); same locality, flowering bushes, 11.viii.1989, (#2646), (1 TMSA); same locality, Naukluft cascades, 12.viii.1989, Endrody-Younga and Klim. (#2648), (4 TMSA). Representative duplicate paratypes deposited in CMNH, FMNH, and MCZ.

Description.—Size (mm × 100; length/width): body 140/60, head 24/42, pronotum 33/54, elytra 90/60. Color brown to dark brown, head and disc of pronotum darker than remainder, setae fine, short; legs and maxillary palpi brown to testaceous. Labrum, in male, with apical margin narrowly upturned, in female simple. Labrum, clypeus, and frons moderately shining, irregularly punctulate. Labroclypeal suture shallow. Shallow oblique fovea in front of each ocellus. Pronotal anterior margin weakly arcuate. Pronotum dull and rather densely paired-punctulate, some forming transverse rows, except smooth and shining, vaguely heart-shaped area on disc. Elytra with serial punctures small, interseries about twice width of punctures; explanate margin narrow in both sexes. Aedeagus (Fig. 58C) with greatly reduced parameres and two elongate distal flagella; length 0.46 mm (from base to bend in flagellum).

Etymology.—Latin, *labrata,* in reference to the distinctive labrum.

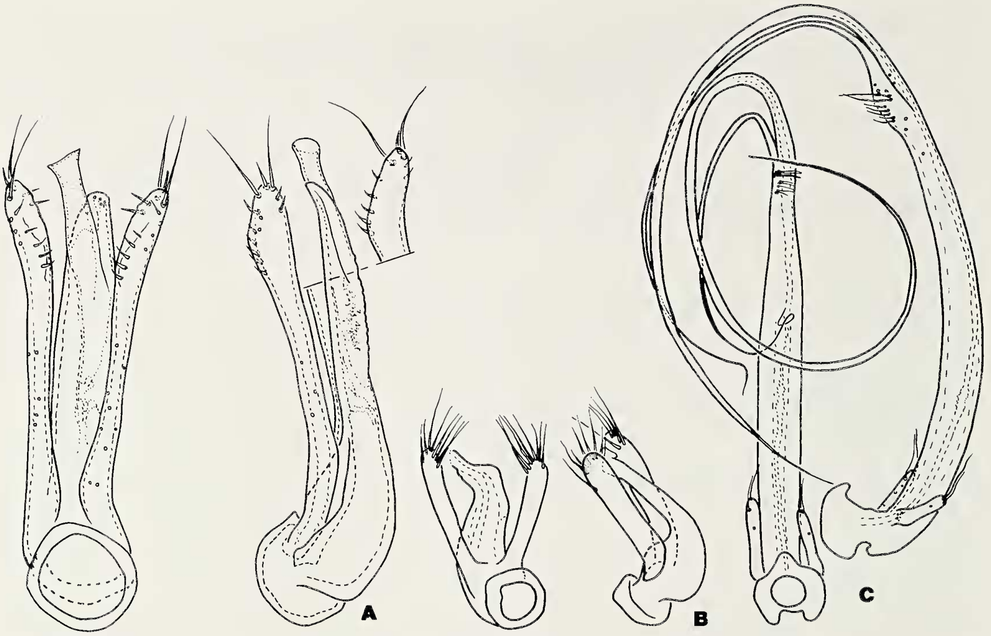


Fig. 58.—Aedeagi of holotypes. A. *Ochtheosus fungicolus.* B. *Davidraena bacata.* C. *Protozantaena labrata.*

Genus *Discozantaena* Perkins and Balfour-Browne
(Fig. 59, 60)

Discussion.—The following description is based on SEM and transparency preparations of *D. genuvela* and an undescribed species from South Africa.

Description.—**Antennal pocket.** A low, rounded hypomeral carina separates the wet- and bubble-hypomeron. The carina becomes obsolete posteriorly. Exocrine pores, about 25–35 in number, are randomly distributed along the inner margin of the carina and between the carina and the reticulate hydrofuge. There are no organized clusters of pores or end-apparatus, and no secretion sulcus exists on the hypomeron.

The antennal pocket setae (Fig. 59:a) are very small, about four in number, nonrigid (lie flat on the cuticle in dry specimens) and located at the posterolateral margin of the antennal pocket. The antennal pocket (Fig. 59:i, 60:i) is relatively wide and shallow, entirely microreticulate, and has a narrow band of hydrofuge pubescence along the lateral, anterior, and anteromedial margins. Within the pocket are randomly distributed exocrine pores.

A prosternal antennal cleaner (Fig. 59:c, 60:c) is located similarly to that of *Parhydraena,* near the anterior margin of the prosternum (but differs slightly in shape and orientation). As in *Parhydraena,* there are no hydrofuge hairs between the antennal cleaner and the antennal pocket, otherwise the antennal cleaner is surrounded by reticulate hydrofuge. Exocrine pores (Fig. 59:p, 60:p) are located near the base of the antennal cleaner.

Periocular exocrine pores (Fig. 60:o) are present at the margin of the eye. The subocular antennal groove is microreticulate and has numerous exocrine pores (Fig. 59:u, 60:u). The postocular area is clothed in hydrofuge pubescence (Fig. 59:t), but lacks any specialized exocrine secretion delivery setae or sensilla.

Madagastrini, **new tribe**

This tribe comprises the genera *Madagaster* n. gen. (type genus), *Davidraena, Gondraena,* and *Coelometopon.* Like the Hydraenidini, this tribe retains several

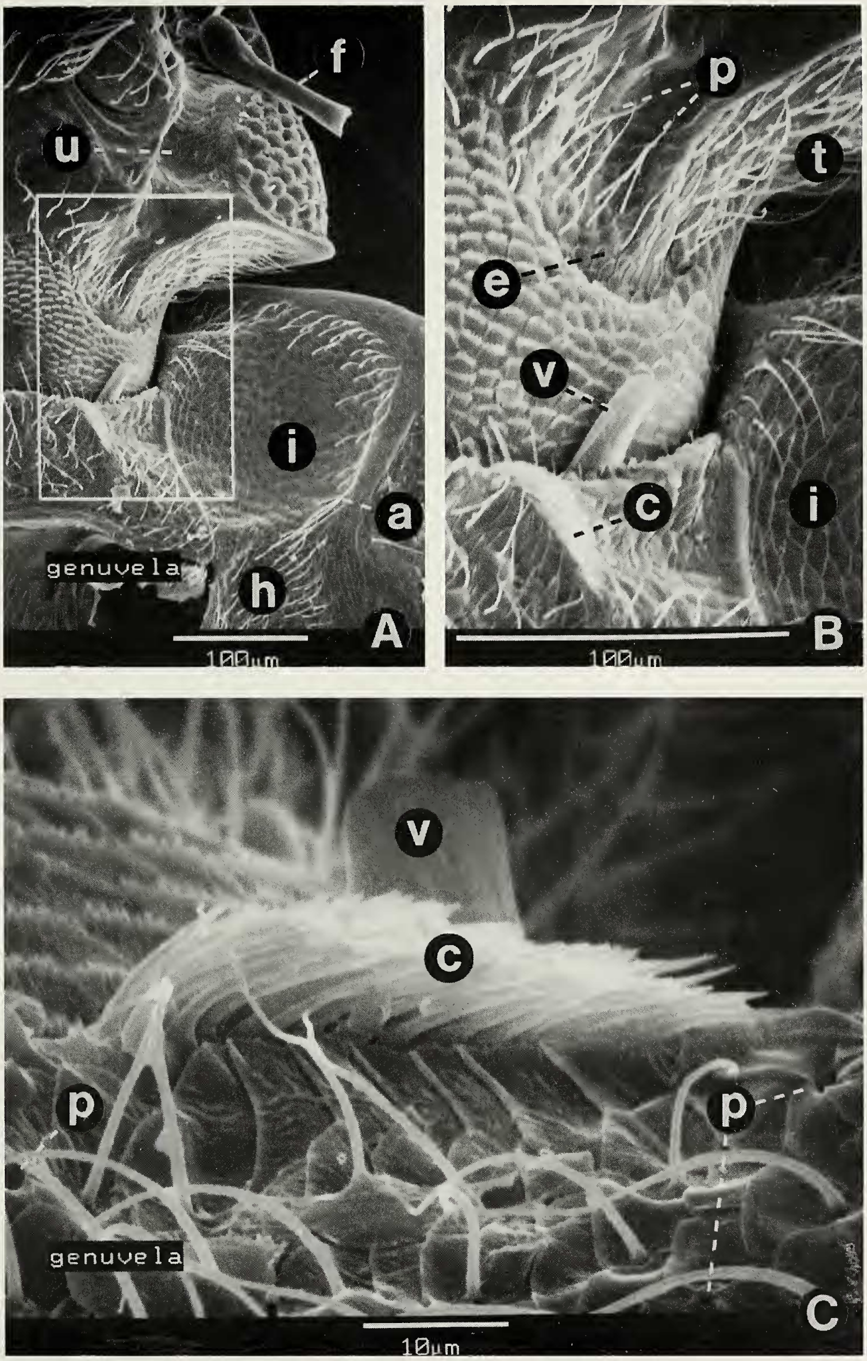


Fig. 59.—*Discozantaena genuvela.* A. Head and prothorax, ventral aspect of left side. B. Rectangular area of A, enlarged. C. Antennal cleaner of prosternum, posteroventral aspect. Structures: (a) hypomeral antennal pocket setae, (c) antennal cleaner of prosternum, (f) first article of antenna (remainder removed), (e) genal antennal groove, (h) hypomeral reticulate hydrofuge, (i) antennal pocket, (p) exocrine pores of (in B) subocular groove and (in C) prosternum, (t) postocular hydrofuge, (u) subocular antennal groove.

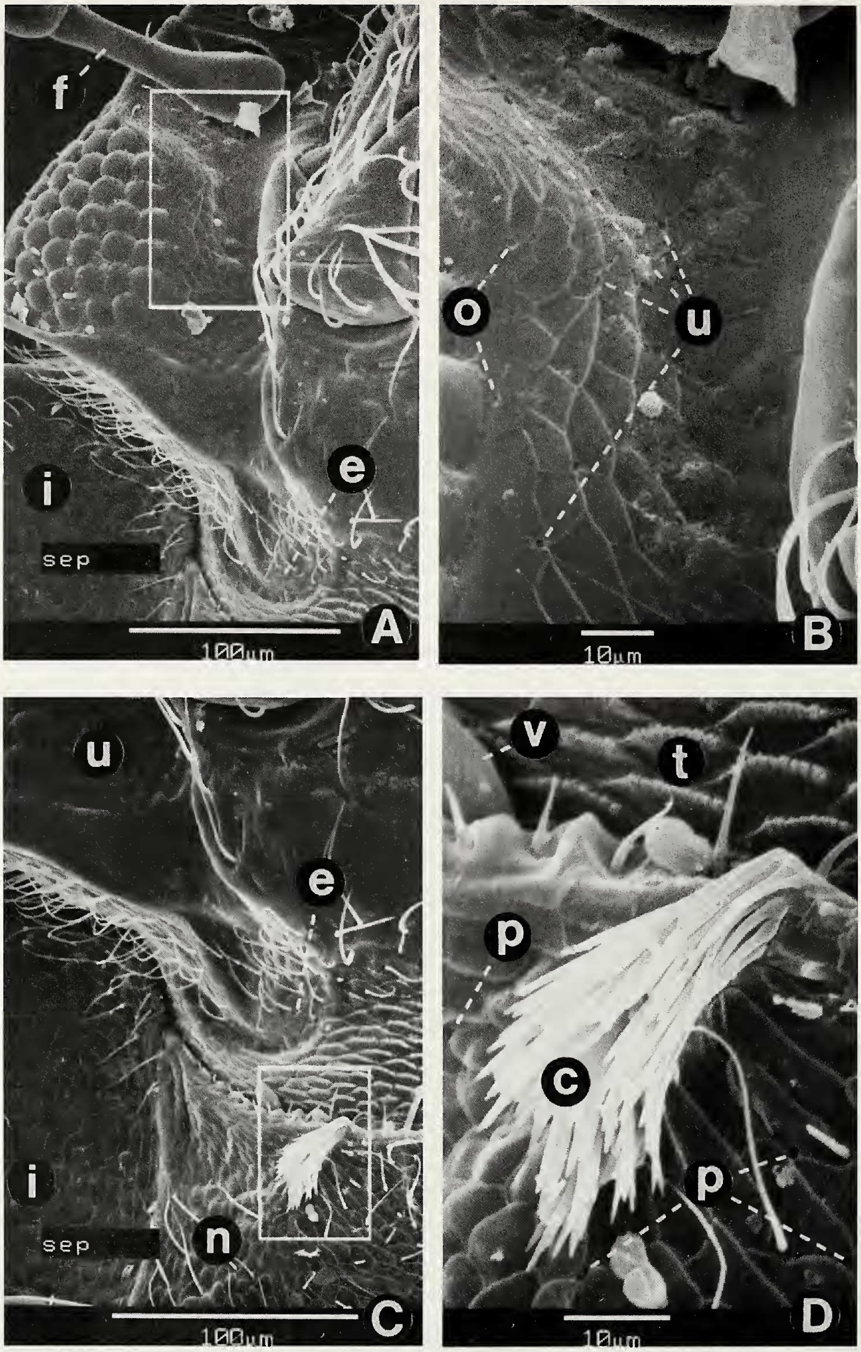


Fig. 60.—*Discozantaena* (undescribed species "SEP," from South Africa). A. Head, ventral aspect of right side. B. Rectangular area of A, enlarged. C. Posterior area of head and adjacent prothorax, ventral aspect of right side. D. Rectangular area of C, enlarged. Structures: (c) antennal cleaner of prosternum, (e) genal antennal groove, (f) first article of antenna (remainder removed), (i) antennal pocket, (n) prosternum, (o) periocular exocrine pores, (p) exocrine pores of prosternum, (t) spiculate microreticulation, (u) exocrine pores of subocular antennal groove, (v) cervical sclerite.

primitive features, and lacks any synapomorphies that could be used to support placing members in other tribes. The geographical distribution of eastern and southern Africa, Madagascar, and southern India is consistent with an ancient Gondwanan (vicariance) distribution.

Members of this tribe have the following hypomeral features: (1) the antennal pocket is located in the anterior face of the hypomeron, at least partially closed ventrally by the anterior extreme of the large wet-hypomeron; (2) the setae on the anteroventral margin of the antennal pocket are moderately large, forming part of the pocket; (3) the nonmarginal setae on the anterior part of the wet-hypomeron are long and flexible; and (4) the hypomeral carina is not contiguous with the notosternal suture, hence the hypomeral hydrofuge attains the antennal pocket.

Like Hydraenidini, members of Madagastrini retain the plesiomorphic condition of 11 antennomeres, a postocular area generally lacking specialized sensilla (but see morphological section for details), and the pronotum has single (nonpaired) punctation. The last sternum, in females, is concealed beneath the sixth (visible) sternum, or only the distal margin exposed. The last sternum is also concealed in males of *Coelometopon,* but is exposed in *Davidraena* and (is huge) in *Madagaster* males. *Madagaster* and *Davidraena* have a band-like strip of reticulation at the medial margin of the antennal pocket, presumably an antennal cleaner.

Coelometopon appears to be a highly specialized member of this tribe, strongly built and with modifications, such as elevated eyes, resulting from selection for a hygropetric existence. Like *Hydraena,* the procoxae of *Coelometopon* are strengthed posteriorly by a joining of the pronotal postcoxal projections with posterolateral extensions of the prosternal process. However, this similarity is clearly convergent: transparency mounts show that in *Coelometopon* the tip of each postcoxal projection fits into a corresponding notch in the prosternal process, whereas the opposite is true in *Hydraena.*

Madagaster is related to other, as yet undescribed, genera from Madagascar. These genera are related to the Madagascar species *Gondraena franzi* and the Indian species *Gondraena indica* (Jäch 1994). *Gondraena* retains many primitive features that are basal for the tribe Madagastrini—including (a) primitive number of antennomeres (11), (b) a deep antennal pocket, (c) nervure intervals of elytra being more-or-less carinate and/or granulate, (d) ventrites 1–4 (entirely) and 5 (basally) with hydrofuge pubescence, and (e) aedeagus simple. A putative synapomorphy, not noted by Jäch (1994), for the type species from India and *Gondraena franzi* (and at least one other undescribed, closely related species in Madagascar) is the form of the antennal club: the last three meres are widened, and the last mere is shorter than the penultimate. Contrastingly, in *Madagaster* the antennal club is elongate, the last mere is longer than the penultimate, only the first two ventrites are entirely hydrofuge pubescent, and the aedeagus is very complex.

Madagaster, new genus

Type Species.—*Madagaster steineri,* new species.

Diagnosis.—Recognized by the 11 articles of the antenna (six + club); the slightly elevated eyes; the ocelli located closer to the midline than to the eyes; the short and robust maxillary palpi with length ratios of last three articles as three : three : four or one : one : one; the transverse, noncordiform pronotum with well-developed postocular emarginations; the elytra with four costae (on homologues of intervals 3, 5, 7, and 9), some interrupted; the costae separated one from the other by three or four rows of punctures; the restricted abdominal hydrofuge pubescence; the apically enlarged and sexually dimorphic abdominal sterna; the very large wet-hypomeron; and the features of the postocular/hypomeral antennal pocket (see morphological section).

Description.—**Antennal pocket.** The hypomeral carina is well defined, angulate posteriorly, and becomes obsolete anteriorly at the antennal pocket. The bubble-hypomeron becomes increasingly narrow anteriorly, very narrow at slightly constricted entrance to antennal pocket.

The wet-hypomeron is very wide, becoming wider from posterior to anterior, reticulate, and with very sparse randomly distributed exocrine pores. Randomly distributed over the anterior fourth are about 12–16 hypomeral setae that are long and flexible, not basally widened. Hypomeral antennal pocket setae, stiffer than the hypomeral setae, about six in number, are submarginally located at the anteromedial angle of the wet-hypomeron. There are no organized clusters of exocrine pores or end-apparatus, and no secretion sulcus exists on the hypomeron. The antennal pocket is large and deep, narrowly opened ventrally. The presumed hypomeral antennal cleaner, a narrow band of scale-like reticulations, is located adjacent to the notosternal suture for its entire length.

A few periocular exocrine pores are present. The subocular antennal groove is deep, its medial margin cariniform; a few exocrine pores (ca. five to ten) are present near the eye margin. The groove is microreticulate except for a small microspiculate area at posterior extreme. A postocular ridge, devoid of hydrofuge pubescence, has about 15 exocrine pores in the lateral part. Between the medial part of the postocular ridge and the eye is a bisinuate, longitudinal ridge bearing, on a prominence at its midlength, a cluster of prominent setae and exocrine pores. A low transverse carina, bearing tiny spicules, divides the area between the eye and the postocular ridge into a smooth anterior part (next to the eye) and a microreticulate posterior part. The postocular area, behind the postocular ridge, is clothed in hydrofuge, but lacks any specialized exocrine secretion delivery setae or sensilla.

Other characters. Size large, body about 2.50–3.00 mm long, form elongate oval, elytra posteriorly truncate, head not deflexed. Antennomeres 11 (six + club), third about as long as combined lengths of fourth to sixth. Maxillary palpi short, length ratios of articles two to four (last) as three : three : four or one : one : one. Eyes well developed, slightly elevated. Labrum set at angle to clypeus, apicomedially deeply incised; anterior margin fringed with long setae. Clypeus anterior margin truncate, straight or slightly emarginate. Ocelli located closer to midline than to eyes, frons with short midlongitudinal sulcus between ocelli, and short oblique fovea at anterior margin of each ocellus; area behind and between ocelli with four low carinae. Pronotum with two narrowly separated, midlongitudinal foveae, anterior about twice as long as posterior, on each side with two oblique admedian and two sublateral foveae; area behind well-developed postocular emarginations and between anterior foveae elevated, tectiform; lateral depressions wide; lateral margin arcuate except weakly sinuate just before base. Anterior hyaline border extremely narrow, lateral and posterior absent. Elytra with four costae (on homologues intervals 3, 5, 7, and 9), some interrupted, the costae separated one from the other by three or four rows of punctures, punctures sometimes not serial. Prosternum in front of procoxae about as long as procoxal cavities, latter narrowly open behind. Intercoxal sternite small, triangular. Legs moderately elongate, tarsi five–five–five. Abdominal sterna five and six enlarged, combined area subequal to or greater than that of first four sterna combined; in males fifth shorter than sixth, seventh very large and completely exposed; in females sixth longer than fifth, seventh very small, entirely retracted beneath sixth or just apical margin visible. Hydrofuge pubescence present on postocular area, bubble-hypomeron (except antennal pockets), notal postcoxal projections, mesosternum, metasternum, first two abdominal sterna, and lateral portions of third and fourth sterna.

Etymology.—Named in reference to the madicolous habitat and the greatly modified abdomen; gender feminine.

Madagaster steineri, new species

Type Material.—Holotype male: Madagascar, Antananarivo, Manakambahiny, in seepage over exposed granite cliff face, 12.i.1990, W. E. Steiner; deposited in the USNM. Fifteen paratypes, five with same data as holotype, ten with same data except date 15.ii.1990, (USNM, CMNH, MCZ).

Description.—Size (mm × 100; length/width): body (length to elytral apices) 299/140, head 51/84, pronotum 66/119, elytra 200/140. Clypeus and frons dull, with dual punctation comprised of very dense micropuctulate ground sculpture and less dense, large punctures, setae short. Labroclypeal suture very deep, at midline with short longitudinal sulcus that nearly connects with similar sulcus at posterior of head. Short, deep sulcus in front of each ocellus. Pronotum with two narrowly separated midlongitudinal fovea, anterior twice as long as posterior; each side with two admedian and two sublateral foveae; lateral margin rounded. Pronotal disc rugosely punctate. Elytral suture costate in posterior. First two elytral "interval" costae (from suture) usually interrupted in two places (sometimes only once), third costa interrupted once, fourth costa not interrupted. Strongly sexually dimorphic: in males, maxillary palpomeres three and four very broad, flattened, and microreticulate on ventral surface, abdominal sterna two to four modified in midline, fifth with posteromedian triangular process, sixth retractable (over median portion) within fifth, seventh large and completely exposed, legs modified. Abdominal sterna five and six enlarged in both sexes, in male combined lengths of two to four equal one-half combined lengths of five and six.

Etymology.—I am pleased to dedicate this distinctive new species to Warren E. Steiner—friend, colleague, and field entomologist extraordinare.

Discussion.—A figure of the male genitalia of *M. steineri,* and descriptions of additional new species in the genus will be given in a separate paper.

Genus *Davidraena* Jäch
(Fig. 61–63)

Diagnosis.—Recognized by the 11 articles of the antenna (six + club), the ocelli located closer to the midline than to the eyes, the pronotum deeply excavate at the posterior angles (Fig. 61), the pronotum and elytra with granulate costae, the broad clypeus that forms a shelf under which the short, robust maxillary palpi are held, the abdominal hydrofuge pubescence restricted to the first two sterna, the very large wet-hypomeron, and the features of the postocular/hypomeral antennal pocket (see morphological section).

Description.—**Antennal pocket.** The hypomeral carina (j in Fig. 61–63) is well defined, angulate posteriorly, and becomes obsolete anteriorly at the antennal pocket. The bubble-hypomeron (h in Fig. 61–63) is very narrow for its entire length.

The wet-hypomeron (w in Fig. 61–63) is very smooth opposite the carina, reticulate anteriorly. The smooth area has very sparse (ca. 15) randomly distributed exocrine pores. Randomly distributed over the anterior fourth are about ten hypomeral setae that are long and flexible, not widened at the base, each with a wide socket. Hypomeral antennal pocket setae (a in Fig. 61–63), about 12 in number, are located on the anterior margin of the wet-hypomeron. There are no organized clusters of exocrine pores or end-apparatus, and no secretion sulcus exists on the hypomeron. The pronotal indentation (Fig. 61B), a deep notch located at the posterior margin of the wet-hypomeron, has a few exocrine pores located along its margin, and the "opening" of the indentation is "closed" by long setae. The antennal pocket (Fig. 63:i) is smooth, large, and deep, but narrowly opened ventrally. The hypomeral antennal cleaner (c in Fig. 61, 63), a narrow band of scale-like reticulations, is located adjacent to the notosternal suture, at the ventromedial margin of the antennal pocket. The inner margin of the antennal pocket bears a dorsomedial setal cluster (Fig. 61, 63D:b) that may be a site of exocrine secretion (substances present in one preparation [Fig. 63D:s] may be artifact).

A few periocular exocrine pores are present. The subocular antennal groove (Fig. 62:u) is deep, its medial margin cariniform, posteriorly the carina forms a prominent genal ridge (g in Fig. 61–63). A few exocrine pores (ca. five) are present in the subocular antennal groove. A postocular ridge (Fig. 62:z) bears a small setal cluster (Fig. 62:y) at the posterior extreme of the subocular groove. The postocular ridge is devoid of hydrofuge pubescence and has about 15 randomly distributed exocrine pores. The postocular area, behind the postocular ridge, is clothed in reticulate hydrofuge (Fig. 62:o), but lacks any specialized exocrine secretion delivery setae or sensilla.

Other characters. Size small, body about 1.35 mm long, form elongate oval, moderately convex, head not deflexed. Antennomeres 11 (six + club), third and sixth (first of club) moderately elongate, subequal to each other in length. Maxillary palpi very short and robust, length ratios of articles two to four (last) as four:three:five, located under shelf of clypeus. Features of antennal pocket as described in morphological section. Clypeus large, anterior margin wide, straight. Ocelli located closer to midline than to eyes, separated by low tumidity behind which are two short longtudinal carinae. Granule-based setae on margin of head and lateral margin of pronotum, except posteroangular excavations. Pronotal disc with two narrowly separated, parallel costae bearing granule-based setae, extended from base to apex. Pronotum transverse, lateral depressions and postocular emarginations well developed,

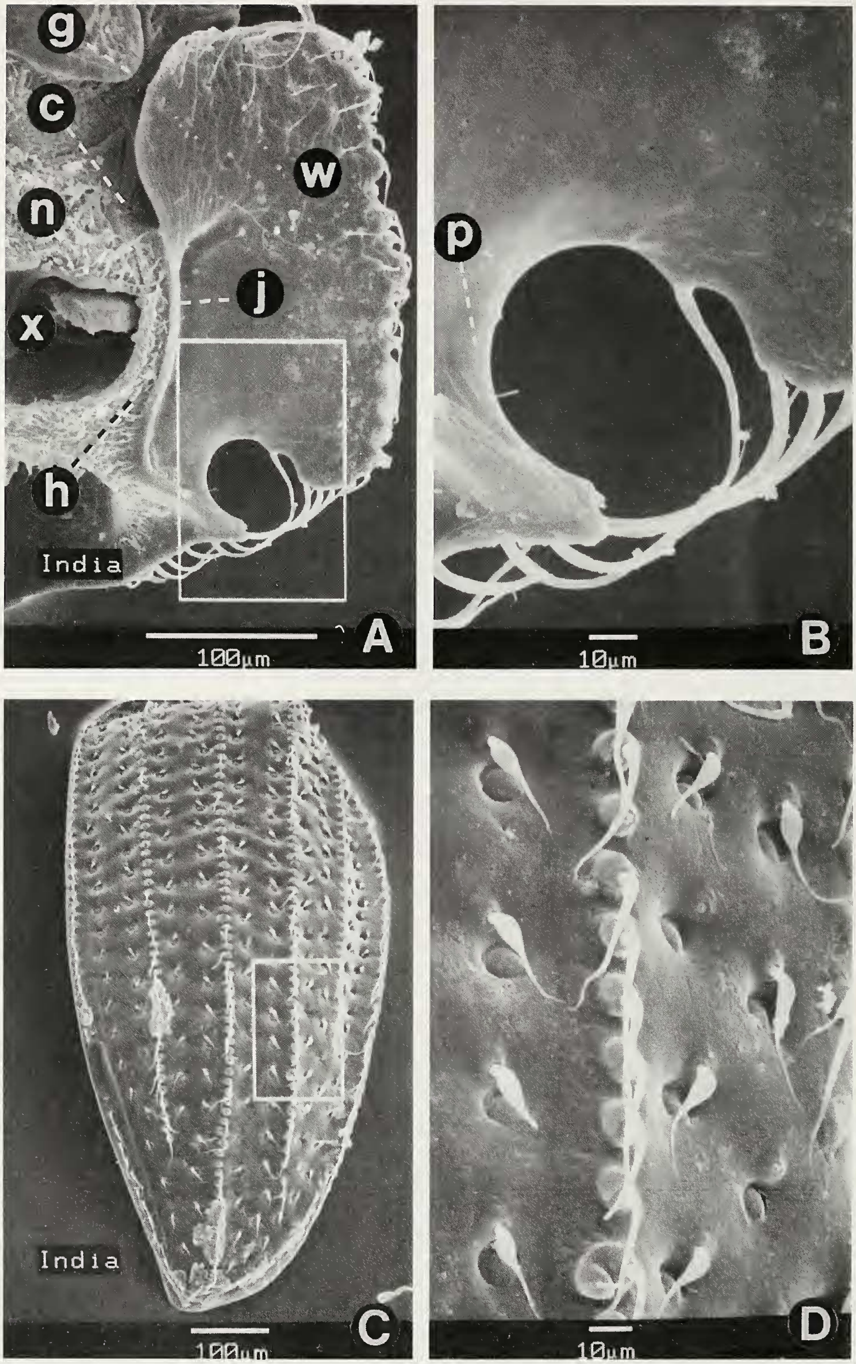


Fig. 61.—*Davidraena bacata.* A. Prothorax, ventral aspect of left side. B. Pronotal indentation (rectangular area of A, enlarged). C. Right elytron. D. Rectangular area of C, enlarged. Structures: (c) antennal cleaner of hypomeron, (g) genal ridge of subocular antennal groove, (h) hypomeral hydrofuge, (j) hypomeral carina, (n) prosternum, (p) exocrine pores at margin of pronotal indentation, (w) wet-hypomeron, (x) procoxal cavity.

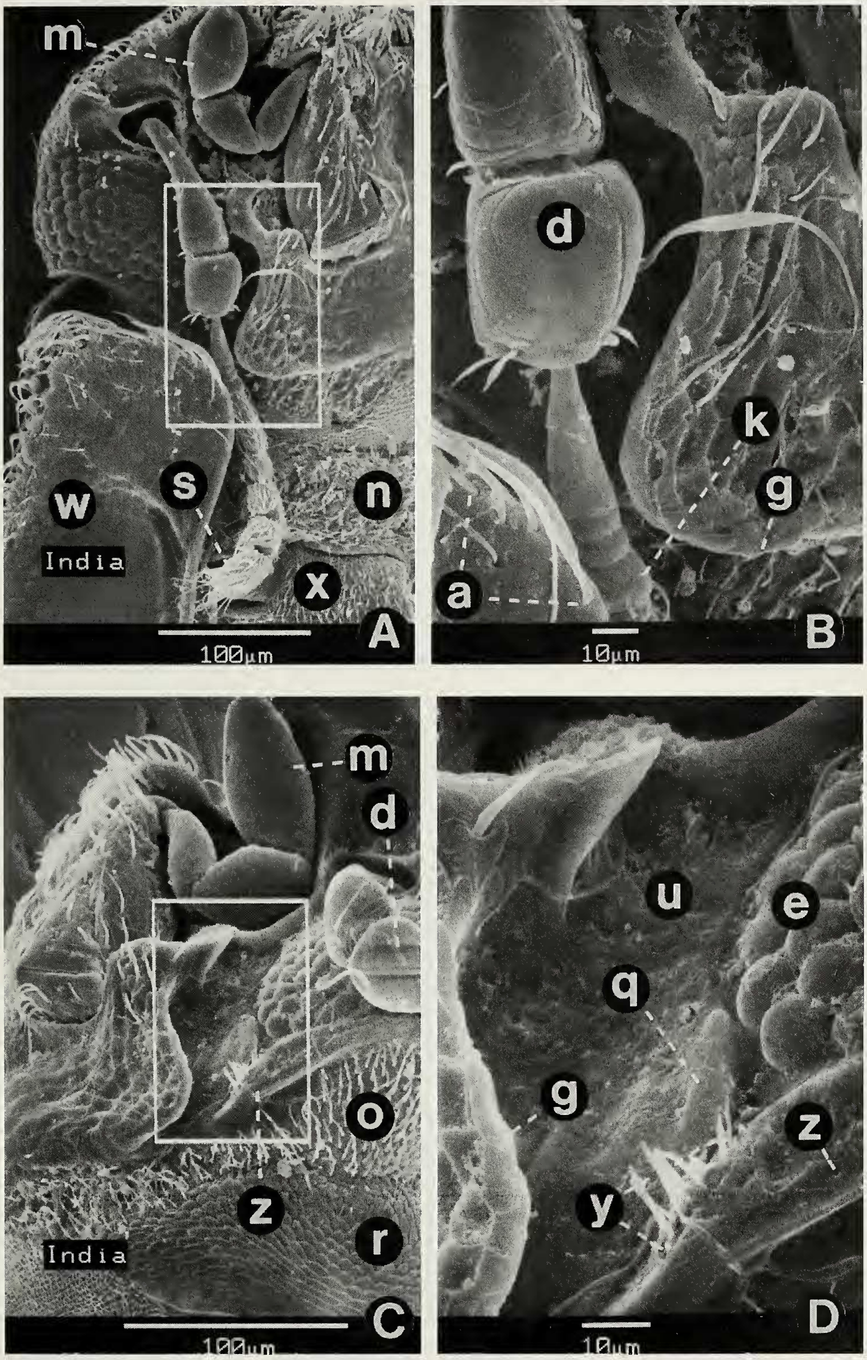


Fig. 62.—*Davidraena bacata.* A. Head and prothorax, ventrolateral aspect of right side. B. Rectangular area of A, enlarged. C. Head, posteroventral aspect of left side. D. Rectangular area of C, enlarged. Structures: (a) hypomeral antennal pocket setae, (d) second antennomere, (e) eye, (g) genal ridge of subocular antennal groove, (k) cupule article of antenna, (m) maxillary palpus, (n) prosternum, (o) postocular hydrofuge, (q) subocular ridge, (r) reticulation, (s) sensilla of antennal club, (u) subocular antennal groove, (w) wet-hypomeron, (x) procoxal cavity, (y) setal cluster of postocular ridge, (z) postocular ridge.

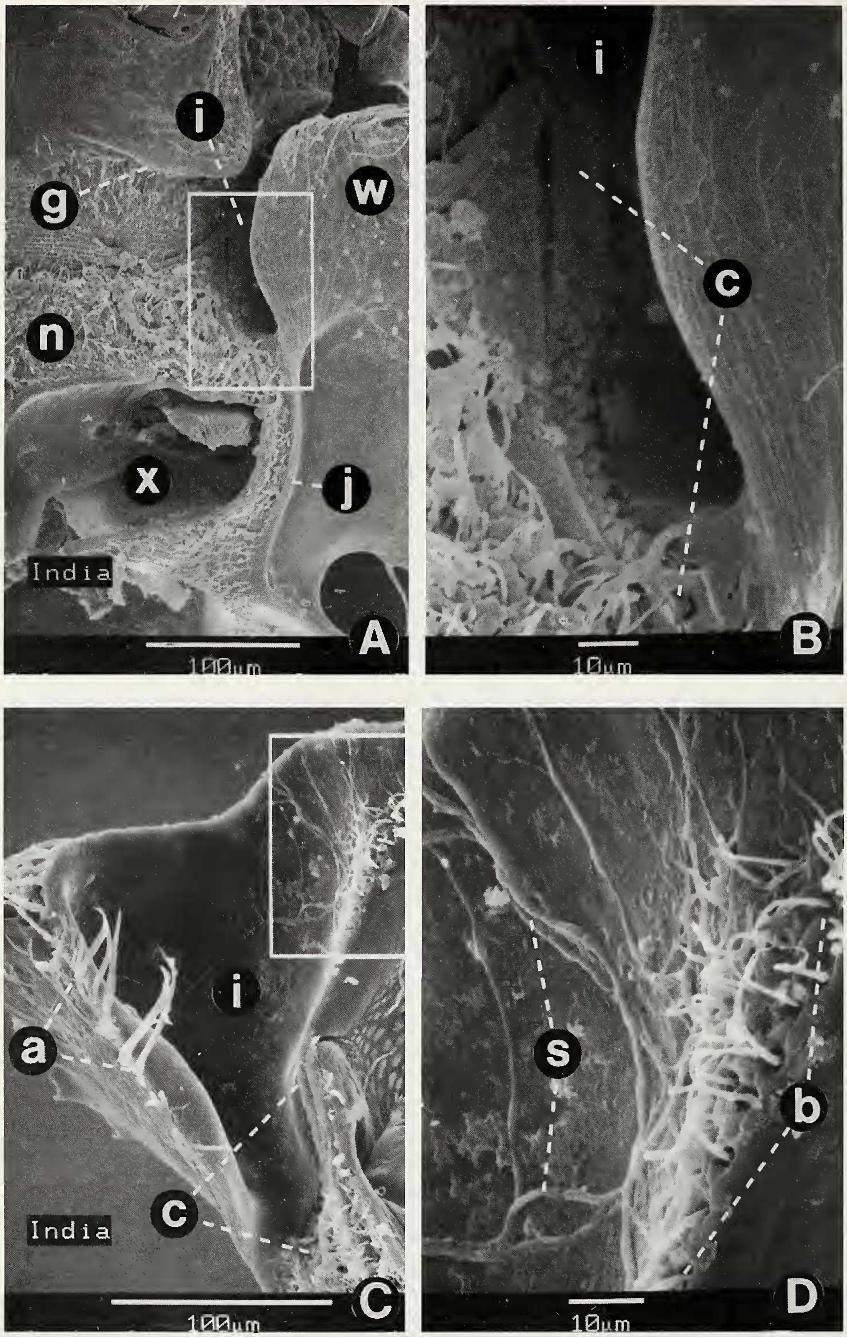


Fig. 63.—*Davidraena bacata.* A. Head and prothorax, ventral aspect of left side. B. Rectangular area of A, enlarged. C. Prothorax, anterior aspect of right side. D. Rectangular area of C, enlarged. Structures: (a) hypomeral antennal pocket setae, (b) dorsomedial setal cluster of antennal pocket, (c) antennal cleaner of hypomeron, (g) genal ridge of subocular antennal groove, (i) antennal pocket, (j) hypomeral carina, (n) prosternum, (s) presumed exocrine secretions, (w) wet-hypomeron, (x) procoxal cavity.

deep excavation at each posterior angle. Anterior hyaline border narrow, lateral and posterior absent. Elytra with ten series of punctures; sutural interval, even-numbered interseries, and lateral margin each costate and bearing unilinear row of granule-based setae. Prosternum shorter than procoxae, latter narrowly open behind. Intercoxal sternite small, triangular. Legs short, tarsi very short, five–five–five. Hydrofuge pubescence present on postocular area, bubble-hypomeron (except antennal pockets), notal postcoxal projections, mesosternum, metasternum, and first two abdominal sterna. First two abdominal sterna short compared to other sterna.

Davidraena bacata, **new species**
(Fig. 58B, 60–63)

Type Material.—Holotype male: India, Kerala, Cardamon Hills, Muttapatti prés Munnan, 1700m, 24.xi.1972, Besuchet, Löbl, Mussard; deposited in MHNG. Paratypes: ten specimens with same data (MHNG, MCZ).

Description.—Size (mm × 100; length/width): body 134/66, head 21/36, pronotum 33/60, elytra 87/66. Clypeus shining, very weakly microreticulate and bearing very small, sparse granules. Sculpture slightly more developed on frons, especially granule-based setae on median tumidity. Pronotum on each side with two oblique costae, parallel to one another, one extended from anterior margin to about midlength, the other extended from base to slightly past midlength; some areas between pronotal costae nonpunctate and strongly shining; posterolateral excavations semicircular and bearing overlapping setae at "entrance." Elytra with noncostate intervals shining, punctures crescent-shaped, each bearing a basally enlarged seta at anterior margin. Metasternal disc very shallowly concave, hydrofuge pubescent. Length ratios of abdominal sterna two to four as one : one : one and one-half : two. Aedeagus (Fig. 58B) with well-developed parameres and lacking distal process or flagellum; length 0.15 mm.

Etymology.—Latin, *bacata* (adorned with pearls), in reference to the rows of elytral granules.

Genus *Coelometopon* Janssens

Discussion.—The following description is based on SEM and transparency mounts of *C. madidum* and two undescribed species from South Africa.

Description.—**Antennal pocket.** The hypomeral carina is distinct, angulate just before the posterolateral angles; anteriorly becoming obsolete at the antennal pocket. The bubble-hypomeron becomes increasingly narrow anteriorly, very narrow at constricted entrance to antennal pocket, where anteromedial angle of wet-hypomeron is produced.

The wet-hypomeron is very wide in the anterior two-thirds, much narrower posteriorly, reticulate, almost lacking exocrine pores. Randomly distributed over the anterior fourth are about 12–16 hypomeral setae that are long and flexible, not basally widened; interspersed with these setae are much shorter, stout, arcuate setae similar to those on lateral margin. Hypomeral antennal pocket setae, about 12–15 in number, are located along the margin of the antennal pocket. There are no organized clusters of exocrine pores or end-apparatus, and no secretion sulcus exists on the hypomeron.

The antennal pocket is large and deep, narrowly opened ventrally, dorsally opened at well-developed postocular emarginations. A short, raised ridge or carina is present in the pocket, on the internal face of the hypomeron. The pocket is hydrofuge pubescent in a narrow band along the medial margin, and more extensively so at the dorsomedial area, otherwise the pocket is smooth and has very sparse exocrine pores. There appear to be no antennal cleaning structures in the pocket or on the prosternum.

Periocular exocrine pores are present. A sparse line of pores is present submarginally along the occipital carina. The subocular antennal groove is deep, its medial margin cariniform; a few exocrine pores are present in the groove and along its lateral margin. The groove is smooth except small spiculate area at the posterolateral extreme (i.e., the ventromedial extreme of the postocular area). The large postocular area is clothed in hydrofuge pubescence, but lacks any specialized exocrine secretion delivery setae or sensilla.

Tribe Limnebiini Mulsant

This group, formerly considered a subtribe (Perkins, 1981), comprises the genera *Limnebius* and *Laeliaena.* The tribe is characterized by (1) the slightly concave hypomeral shape, lacking a hypomeral carina, and having a short row of antennal pocket setae; (2) the smooth dorsal habitus; (3) the proportions of the antennae;

and (4) the shape and chaetotaxy of the mentum. The structure of the hypomeron and the mentum suggest a closer relationship with the Parhydraenini than with the Hydraenini.

Genus *Laeliaena* Sahlberg

Discussion.—This is a very rare genus, known only from a few specimens of two species from Turkestan and northern India. I have been able to study only a single transparency mount of an undescribed species from Nepal, plus one dry specimen of the type species *L. sparsa* J. Sahlberg. *Laeliaena* was proposed as a sister group to *Limnebius* by Perkins (1981:430), being similar in smooth dorsal habitus and in the form of maxillary palpi and antennae, but differing in having a less derived pronotal shape. This placement is strengthened by the hypomeral shape, and the separation of *Laeliaena* as a distinct genus is corroborated by the absence of a specialized ESDS.

Description.—**Antennal pocket.** The general shape of the hypomeron is very similar to that of *Limnebius* and, like that genus, a hypomeral carina is lacking and a short row of antennal pocket setae is present. However, there is no hypomeral glandular fovea, no exocrine gland cluster, and no distinct row of marginal setae bordering the hydrofuge hypomeron (i.e., no specialized ESDS). Additionally, the postocular area lacks antennal pocket setae.

Subfamily Prosthetopinae Perkins

The diagnostic features of the tribes and genera of this subfamily are given by Perkins and Balfour-Browne (1994). In contrast to the Ochthebiinae and Hydraeninae, characters of the antennal pocket and hypomeron are conservative in the Prosthetopinae. However, the subfamily is very diverse in other external features—consistent with the benthic microhabitat of many members (discussed in Perkins and Balfour-Browne, 1994).

Genus *Nucleotops* Perkins and Balfour-Browne
(Fig. 64, 65)

Discussion.—The following description is based on SEM and transparency mounts of *N. nimbaceps.* Two new species of *Nucleotops* from South Africa will be described in a separate publication.

Description.—**Antennal pocket.** The hypomeral antennal pocket (Fig. 64:h, 65:h) is a very shallow depression on the anterior face of the hypomeron. In the aquatic genera the pocket is hydrofuge pubescent (Fig. 65A), whereas in the humicolous genus *Nucleotops* (Fig. 64C) the setae are spiniform. The pocket setae are contiguous with the pubescence of the prosternum, but not with that of the postcoxal projection.

The hypomeral carina (Fig. 64:e, 65:e) is well developed. Over its middle third the carina is contiguous with the notosternal suture, hence the hydrofuge pubescence of the antennal pocket and that of the postcoxal projection are not contiguous. Generally, a few (two to ten) exocrine pores are present along the part of the carina that borders the antennal pocket.

The wet-hypomeron (Fig. 64:w) is wide, varying from smooth to strongly microreticulate, and has random exocrine pores that vary in density and placement according to the species. There are neither organized clusters of pores, nor a secretion sulcus on the hypomeron. Antennal pocket setae are lacking, but in members of aquatic genera the anterior part of the wet-hypomeron has a few hypomeral setae (Fig. 65A:s) that vary in number (ca. four to ten) and length (very short to moderately long) depending on the taxon.

Periocular exocrine pores are present. The subocular antennal groove (Fig. 64:u, 65:u) is well developed, weakly microreticulate; along its medial margin are about five to ten randomly spaced exocrine pores. The lateral margin of the groove is cariniform in *Nucleotops* (Fig. 64A:r, 64B:r), smooth in the other genera (Fig. 65A).

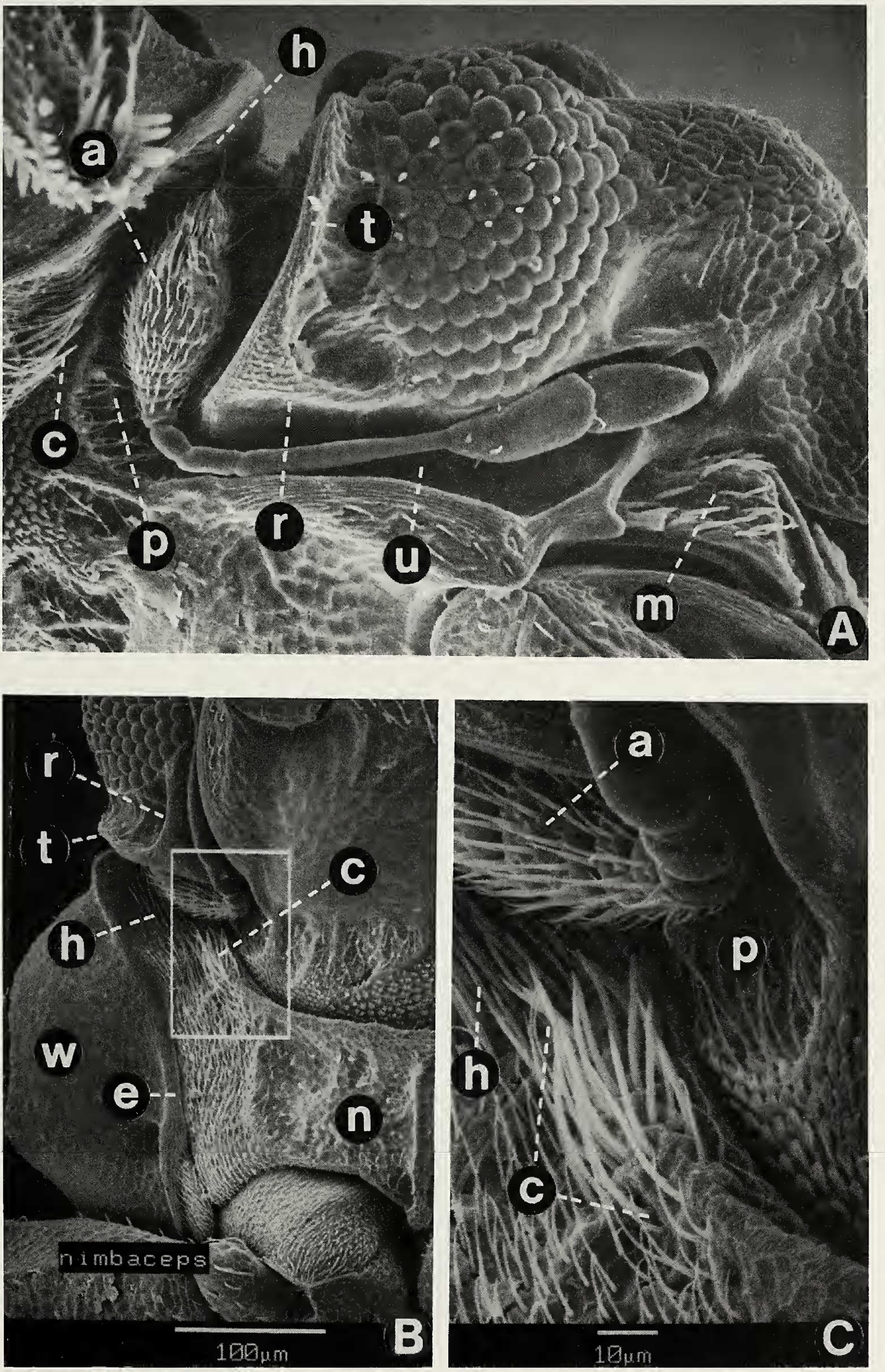


Fig. 64.—*Nucleotops nimbaceps*, head and prothorax, right side. A. Ventrolateral aspect. B. Ventral aspect. C. Detail of antennal cleaner and antennal club (rectangular area of B, enlarged). Structures: (a) antennal club,(c) prosternal antennal cleaner, (e) hypomeral carina, (h) antennal pocket, (m) mandible, (p) postocular antennal pocket, (r) lateral carina of antennal groove, (t) postocular carina, (u) subocular antennal groove, (w) wet-hypomeron.

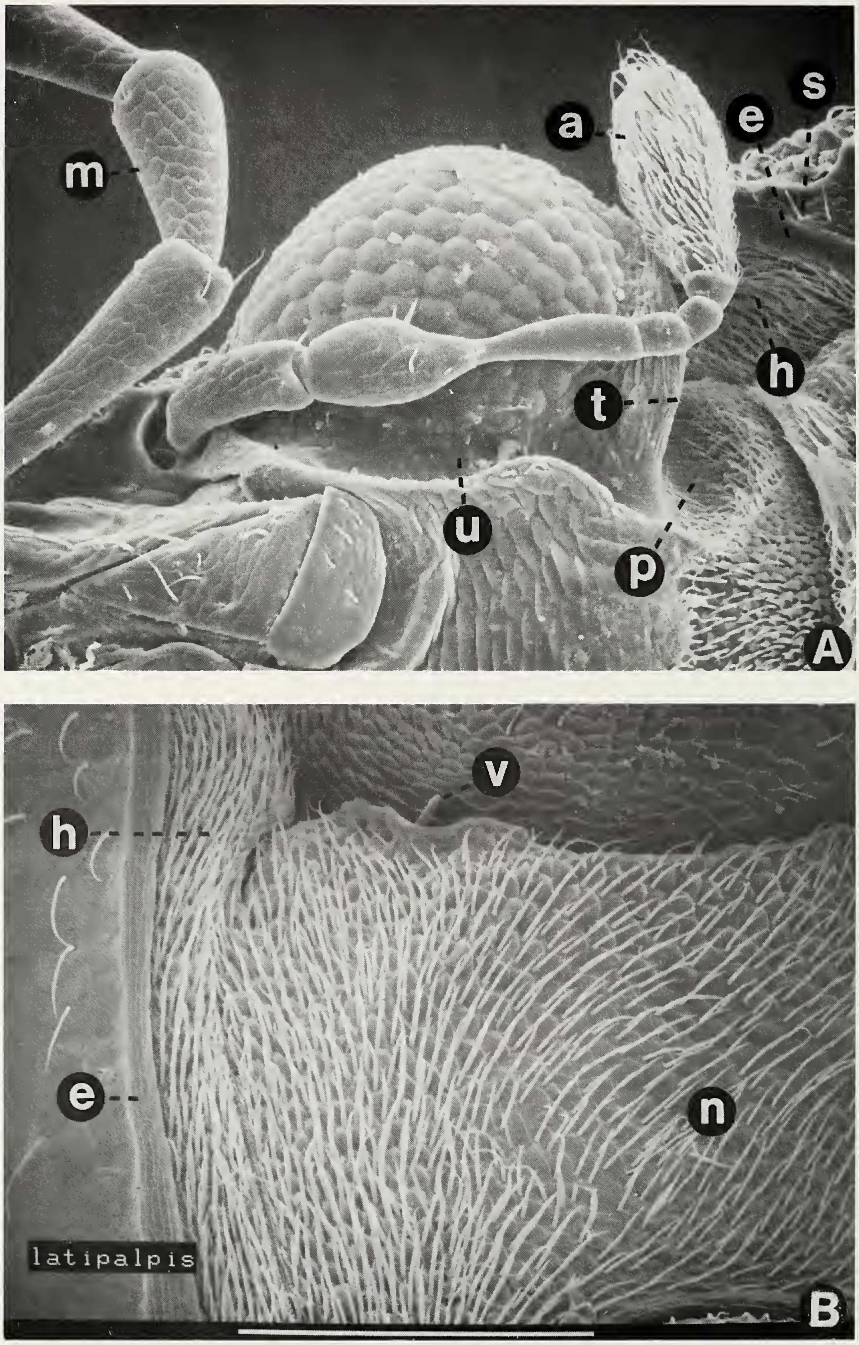


Fig. 65.—A. *Parasthetops nigritus*, ventral aspect of left eye and associated structures. B. *Podaena latipalpis*, venter of prothorax, right side. Structures: (a) antennal club, (e) hypomeral carina, (h) hydrofuge hypomeron, (m) maxillary palpus, (n) prosternum, (p) postocular antennal pocket, (s) hypomeral setae, (t) postocular carina, (u) subocular antennal groove, (v) cervical sclerite.

The postocular antennal pocket (Fig. 64:p, 65:p) is formed by the shallowly concave area behind the eye, and by a contiguous, small concavity on the gena. The pocket is bordered by a distinct postocular carina (Fig. 64:t, 65:t). Setae in the postocular part of the antennal pocket are of the hydrofuge type in the aquatic species, spiniform in *Nucleotops*. The remainder of the pocket (on the gena) may be reticulate and devoid of setae (Fig. 65A:p). The postocular area lacks any specialized exocrine secretion delivery setae or sensilla. In *Nucleotops*, the prosternal antennal cleaner (Fig. 64: c), a cluster of spiniform setae, is located on the anterior margin of the prosternum, adjacent to the antennal pocket.

Orchymontinae, **new subfamily**

This new subfamily is erected for the New Zealand endemic genera *Orchymontia* (type genus), *Podaena*, and *Homalaena*; these three genera are similar in the basic morphology of the postocular area and the hypomeron. Members of this subfamily are diagnosed by the following features: (1) hypomeral antennal pockets virtually absent, area clothed with hydrofuge; (2) gena with a shallow antennal pocket that is laterally limited by the horizontally oriented temporal lobe (hence head is not retractile to level of eyes); (3) dorsum of head at margin of eye with whip-like setae set in a reticulate field; (4) antennae retaining ancestral configuration of basal meres, apical (club) meres reduced, lacking hydrofuge pubescence; (5) last sternum, in females, concealed beneath the penultimate sternum; and (6) head with tentorium elongate and with laminatentoria not fused on meson (see discussion under Ochtheosini).

Derived features of this group include specialized supraocular whip-like setae set in a supraocular reticulate field (Fig. 67B:s, f; 69B:s, f); a reduced, entirely nonpubescent antennal club (Fig. 68A:a, 69D:a); and very dense, short, ventral vestiture (Fig. 70), probably plastron-forming. In some species the facets on the posterior part of the eye are reduced, forming a shallow ocular impression (Fig. 68B:i) that appears to conform to the path of movement of the antenna.

Genus *Podaena* Ordish
(Fig. 66–70)

Discussion.—The following description is based on SEM preparations of *P. maclellani* (Zwick) and *P. latipalpis* Ordish, in addition to transparency mounts of *P. dentipalpis, Orchymontia ciliata* Ordish, and *Homalaena dispersa* Ordish.

Description.—**Antennal pocket.** A well-developed, rounded hypomeral carina (Fig. 66:e, 68:e) separates the wet- and the much smaller bubble-hypomeron. There is no antennal pocket. However, the bubble-hypomeron, a narrow band opposite the prosternum (Fig. 66E:h), widens anteriorly and continues into the area normally occupied by the antennal pocket (h in Fig. 66A, B, C).

The wet-hypomeron (Fig. 66A:w) is wide, smooth, and has sparse, random exocrine pores that vary in number according to the species (e.g., 10–20 in *O. spinipennis* and *P. dentipalpis*, 40–50 in *H. dispersa*. There are neither organized clusters of pores, nor a secretion sulcus on the hypomeron. Antennal pocket setae are entirely lacking.

Periocular exocrine pores are present. The subocular antennal groove (Fig. 67:u, 68:u) is well developed, weakly microreticulate; along its medial margin are about 10–14 random exocrine pores.

An oval, shallow, genal antennal pocket (Fig. 67:g, 68:g) is located at the end of the subocular antennal groove. The posterior part of the pocket has asperite hydrofuge and exocrine pores (Fig. 67D, 68D); the remainder of the ventral surface of the head lacks hydrofuge pubescence. A postocular ridge (r in Fig. 67–69) forms the lateral margin of the genal antennal pocket. The postocular area lacks any specialized exocrine secretion delivery setae or sensilla.

KEYS TO TAXA

The following diagnostic keys are given below: (1) Key to Subfamilies; (2) Key to Tribes and Genera of Hydraeninae; and (3) Key to Tribes, Subtribes, and

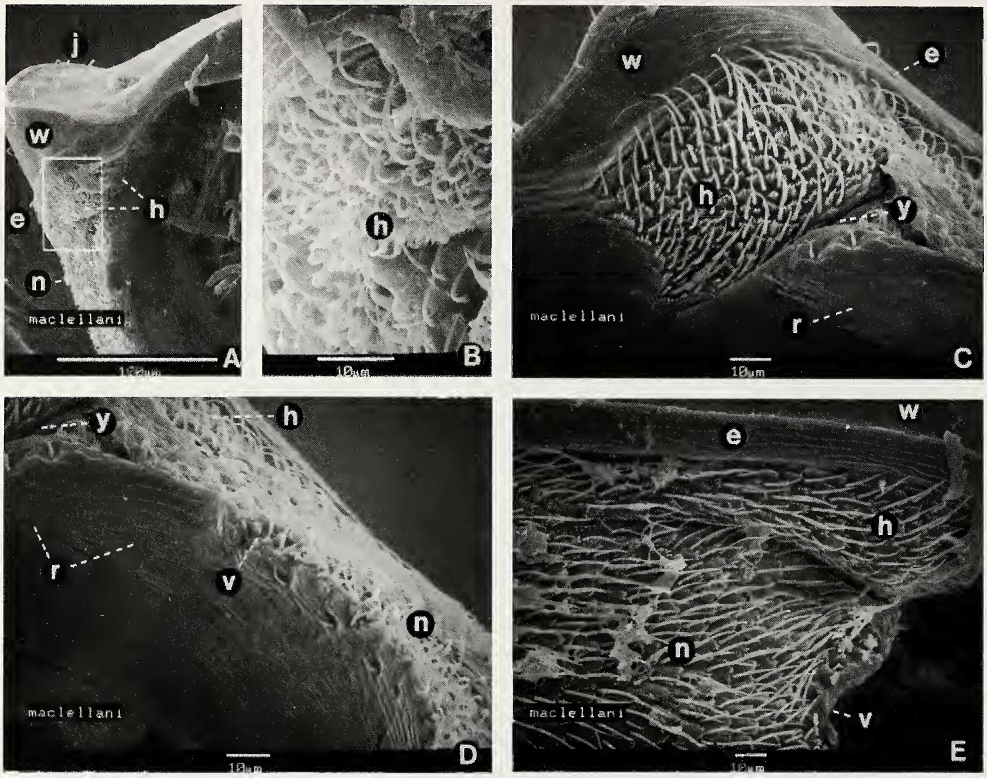


Fig. 66.—*Podaena maclellani*, prothorax. A. Anterior aspect of right side. B. Rectangular area of A, enlarged. C. Anteroventral aspect of hypomeron, left side. D. Cervical area of prosternum, left side. E. Hypomeron and prosternum, ventral aspect of right side. Structures: (e) hypomeral carina, (h) hypomeral asperite hydrofuge, (j) anterolateral area of pronotum, (n) prosternum, (r) reticulations of cervical area, (v) emargination of prosternum for cervical sclerite, (w) wet-hypomeron, (y) suture between prosternum and hypomeron.

Genera of Ochthebiinae. Keys to the genera of Orchymontinae are given by Ordish (1984), and to the taxa of Prosthetopinae by Perkins and Balfour-Browne (1994).

Key to Subfamilies

1. Hypomeral antennal pocket absent or at most a shallow depression on anterior face of hypomeron, lacking pocket-forming setae (Fig. 64B, 66A); antennal club reduced and/or articles tightly joined (Fig. 65A, 68A); ventral vestiture very short and dense (except some humicolous forms), often plastron-forming (Fig. 70A) 2

1′. Hypomeral antennal pocket varying from well-formed depression in anterior face of hypomeron (Fig. 15A) to more open concavity of hypomeron, either hydrofuge pubescent or with pocket-forming setae or hyaline ridges associated with bubble formation (Fig. 1A, 26A, 41A); antennal club longer, articles loosely articulated (Fig. 1A, 41A); ventral vestiture generally less dense, longer, hydrofuge (Fig. 1C) 3

2. Hypomeral antennal pockets absent, nonpubescent antennal club held in shallow, genal antennal pocket that is laterally limited by horizontally oriented temporal lobe (Fig. 68A); hypomeral carina separated from notosternal suture by bubble-hypomeron (Fig. 65B); head with supraocular whip-like setae set in reticulate field (Fig. 67A, B; 69A, B); mesosternal plaques absent . . . . Orchymontinae, new subfamily

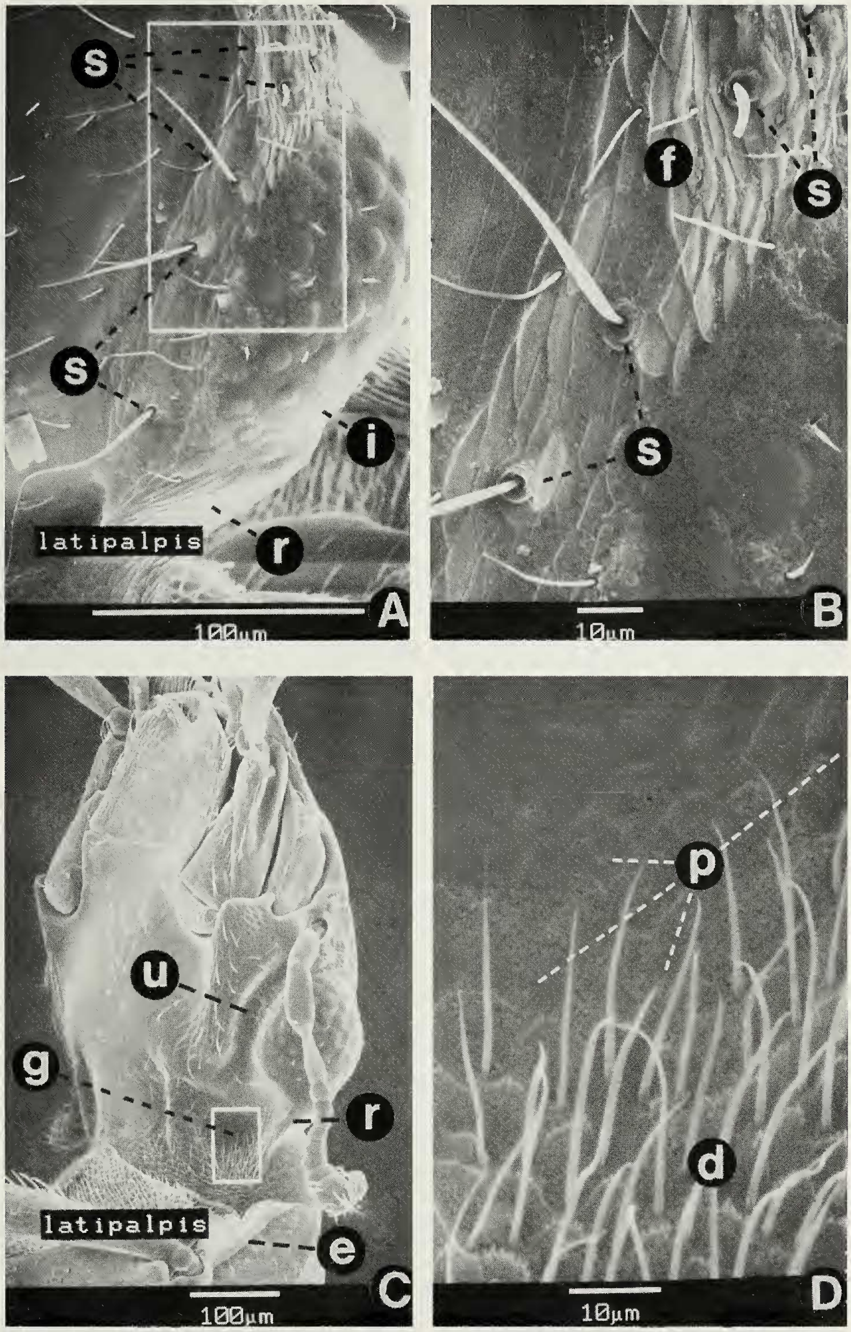


Fig. 67.—*Podaena latipalpis,* head. A. Supraocular area. B. Whip-like setae (rectangular area of A). C. Head, ventrolateral aspect. D. Genal antennal pocket (rectangular area of C). Structures: (d) asperite hydrofuge, (e) hypomeral carina, (f) supraocular reticulate field, (g) gular antennal pocket, (i) ocular impression, (p) exocrine pores of gular antennal pocket, (r) postocular ridge, (s) supraocular whip-like setae, (u) subocular antennal groove.

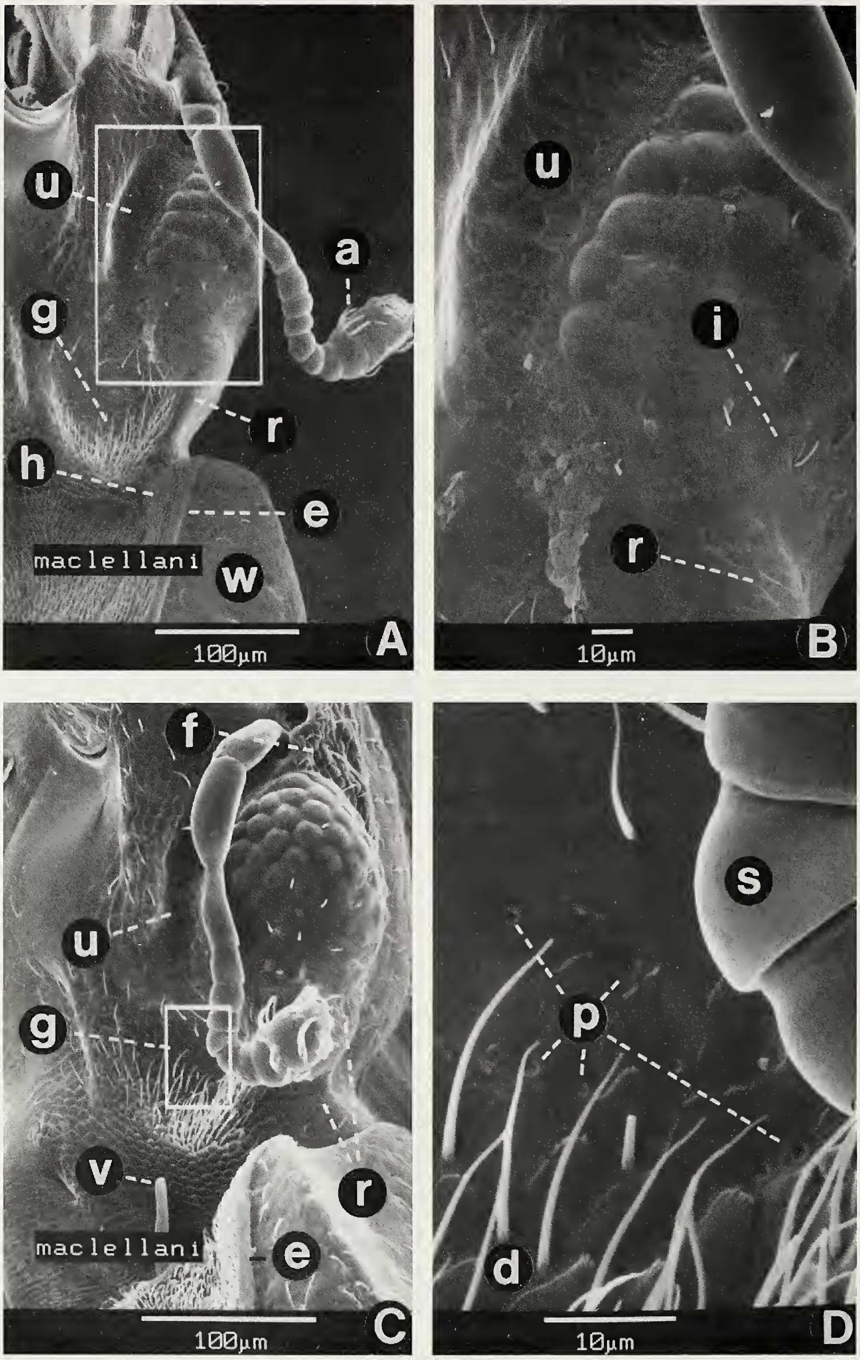


Fig. 68.—*Podaena maclellani,* head and prothorax, left side. A. Ventral aspect. B. Eye and adjacent structures (rectangular area of A). C. Ventrolateral aspect. D. Genal antennal pocket (rectangular area of C). Structures: (a) sensilla of antennal club, (d) asperite hydrofuge, (e) hypomeral carina, (f) supraocular reticulate field, (g) gular antennal pocket, (i) ocular impression, (p) exocrine pores of gular antennal pocket, (r) postocular ridge, (s) seventh antennomere, (u) subocular antennal groove, (v) cervical sclerite.

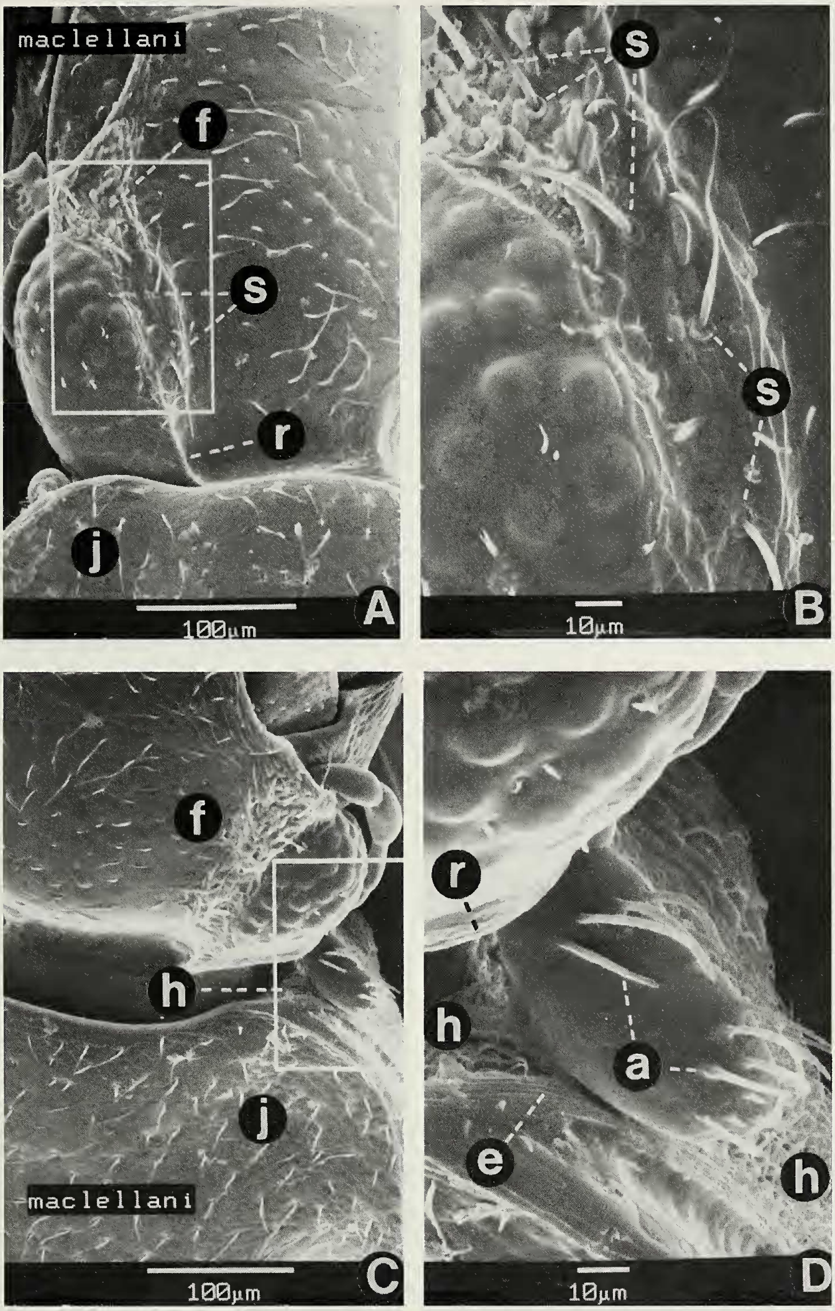


Fig. 69.—*Podaena maclellani,* dorsum of head and adjacent prothorax. A. Supraocular area. B. Whip-like setae (rectangular area of A). C. Oblique aspect. D. Antennal club and adjacent structures (rectangular area of C). Structures: (a) sensilla of antennal club, (e) hypomeral carina, (f) supraocular reticulate field, (h) hydrofuge hypomeron, (j) anterolateral angle of pronotum, (r) postocular ridge, (s) supraocular whip-like setae.

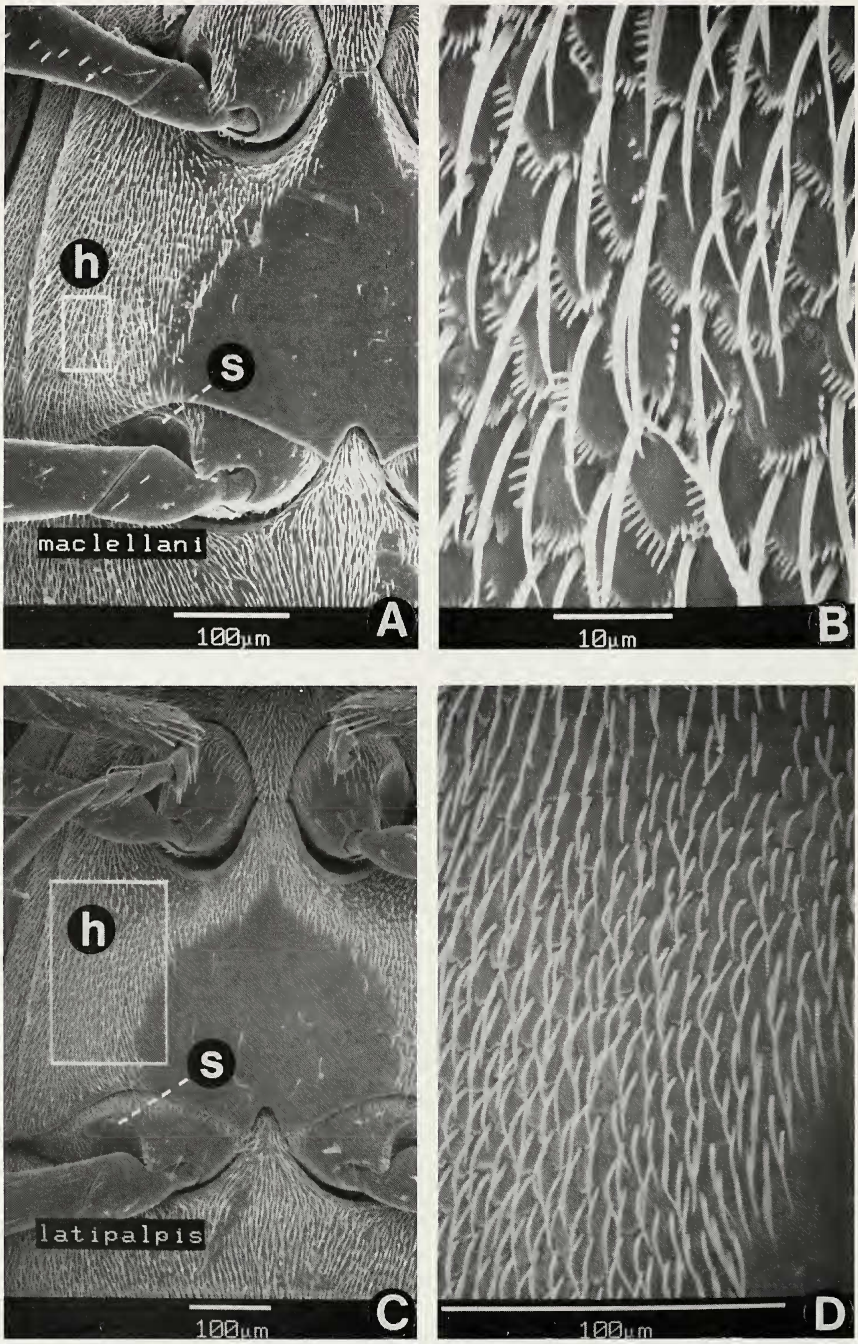


Fig. 70.—*Podaena,* metasternum and adjacent structures. A. *P. maclellani.* B. Vestiture (rectangular area of A). C. *P. latipalpis.* D. Vestiture (rectangular area of C). Structures: (h) hydrofuge or plastron vestiture, (s) metacoxal sensillum.

2′. Hypomeral antennal pockets very shallow, pubescent antennal club held behind eye, in postocular antennal pocket (Fig. 64A); hypomeral carina contiguous with median portion of notosternal suture, separating bubble-hypomeron into anterior and posterior parts (Fig. 64B); head lacking supraocular whip-like setae; mesosternum with submedian pair of plaques, sometimes joined to form inverted Y-shape . . . . Prosthetopinae Perkins

3. Hypomeral antennal pocket in ventral face of hypomeron, bordered medially by notosternal suture (Fig. 1A, 42A, 44A, 48A); penultimate maxillary palpomere more robust and longer than ultimate (Fig. 30C); specialized ESDS gland concentration in head . . . . Ochthebiinae Thomson

3′. Hypomeral antennal pocket in anterior face of hypomeron, generally anterior to most of notosternal suture, with lateral portion of pocket formed by extensive wet-hypomeron (Fig. 18A, 52C, 54A, 63A), or specialized hypomeral antennal pocket setae (Fig. 26A, 57A); penultimate maxillary palpomere neither longer than nor more markedly robust than ultimate; specialized ESDS gland concentration in prothorax . . . . Hydraeninae Mulsant

Key to Tribes and Genera of Hydraeninae

1. Hypomeral antennal pocket formed by stiff, arcuate hap-setae (Fig. 26A:e, 57A:a; secondarily reduced in *Discozantaena*); anterior part of wet-hypomeron not enclosing antennal pocket (except *Pneuminion*) 2

1′. Hypomeral antennal pocket, at anterior extreme, formed by wet-hypomeron, which may bear hap-setae on medial margin (Fig. 10A, B; 18A; 54A; 61A) 7

2. Hypomeron slightly to markedly concave, lacking hypomeral carina, anteriorly with short row of hap-setae (Fig. 26A); dorsum smooth, quite evenly convex; pronotal foveae absent or indistinct, punctures not paired; antenna with nine articles (four + club), second article slightly longer than first, about twice length of second; antennal club with each article slightly larger than preceding; prosternum lacking antennal cleaner (Limnebini Mulsant) 3

2′. Hypomeron not concave, except at antennal pocket, with or without hypomeral carina (Fig. 57C); dorsum not evenly convex, pronotum with distinct impressions and paired punctures; antenna with either ten or 11 articles (five or six + club), second article shorter than first, not twice as long as third; antennal club with second article slightly smaller than first; prosternum anterolaterally with cluster of sharp spines (antennal cleaner?) (Fig. 57A:c, 59B: c; Parhydraenini new tribe) 4

3. With ESDS components: hypomeral glandular fovea, marginal setae of hydrofuge hypomeron, and postocular antennal pocket setae (Fig. 26, 27); pronotum widest basally, body contour uninterrupted; antennal club more loosely articulated, each article larger than preceding; aquatic species; nearly cosmopolitan . . . . *Limnebius* Leach

3′. Lacking ESDS components cited above; pronotum narrowed basally, body contour interrupted between prothorax and elytra; antennal club with last three articles tightly joined to form oval outline distinctly larger than basal two articles; aquatic species; Turkestan, India, and Nepal . . . . *Laeliana* Sahlberg

4. Anterior extreme of wet-hypomeron enclosing part of antennal pocket; pronotum anterior margin with distinct postocular emarginations; antenna with 11 articles (six + club); aquatic species; South Africa . . . . *Pneuminion* n. gen.

4′. Wet-hypomeron not enclosing antennal pocket (Fig. 57A); pronotum anterior margin lacking postocular emarginations; antenna with ten articles (five + club) 5

5. Hypomeral antennal pocket bordered posteriorly with sparse, indistinct, flexible setae that lie on cuticle in dry specimens (Fig. 59A:a); pronotum explanate, widest slightly behind middle, then markedly attenuate to posterolateral angles, each of which is produced in small acute point; explanate margin of elytron very wide, in habitus view concealing tibiofemoral articulation; maxillary palpi and tarsi very short; humicolous species; South Africa . . . . *Discozantaena* Perkins and Balfour-Browne

5′. Hypomeral antennal pocket bordered posteriorly with long, stiff, arcuate setae (Fig. 57D:a); pronotum widest near midlength, posterolaterally subrectangulate; maxillary palpi and tarsi of various lengths 6

6. Hypomeral carina absent; maxillary palpus large, as long as antenna, apical article wide, inner surface arcuate at base; aedeagus with long terminal flagellum and very short parameres; aquatic species; South Africa . . . . *Protozantaena* n. gen.

6′. Hypomeral carina separating wet- and bubble-hypomeron (Fig. 57C:b); maxillary palpi of various lengths, not shaped as above; aedeagus not as above; aquatic and humicolous species; eastern and southern Africa . . . . *Parhydraena* Orchymont

7. Prosternal intercoxal process expanded laterally behind procoxae, closing procoxal cavities by interlocking with postcoxal pronotal projections (Fig. 52C), tip of each lateral projection of intercoxal process fitting into small notch in corresponding postcoxal pronotal projection; second article of maxillary palpus elongate and slender (Fig. 15C); last sternum of females with pair of sensory clusters; anterior part of wet-hypomeron lacking elongate flexible setae; antenna with nine or ten articles (four or five + club; Hydraenini Mulsant) 8

7′. Prosternal intercoxal process not expanded laterally behind procoxae (Fig. 63A), or if procoxal cavities closed (*Coelometopon*), then each lateral projection of intercoxal process with notch into which fits corresponding tip of postcoxal pronotal projection; second article of maxillary palpus not elongate and slender; last sternum of females lacking pair of sensory clusters; anterior part of wet-hypomeron with elongate flexible setae (Fig. 54A:a, 61A); antenna with 11 articles (six + club) 9

8. Hypomeron with ESDS sulcus; bubble-hypomeron not lobe-shaped anteriorly; antennal pocket with antennal cleaner (Fig. 12A, 13A, 15A); gena with stiff gap-setae (Fig. 19A:b); labrum and mandible with interlocking mechanism; mentum with apicomedian process; antenna with nine articles (four + club); aquatic species; cosmopolitan . . . . *Hydraena* Kugelann

8′. Hypomeron lacking ESDS sulcus; bubble-hypomeron lobe-shaped anteriorly (Fig. 52C); antennal pocket lacking antennal cleaner; gena with elongate, flexible setae (Fig. 53B:g), lacking stiff gap-setae; labrum and mandible lacking interlocking mechanism; mentum with apicomedian notch; antenna with ten articles (five + club); aquatic species; Venezuela . . . . *Adelphydraena* Perkins

9. Hypomeral carina contiguous with (or nearly so) notosternal suture (Fig. 54B), hydrofuge pubescence restricted to postcoxal pronotal projection; setae on margin of wet-hypomeron at opening to antennal pocket very small, not pocket-forming; last sternum of female exposed and bearing setae; South America (Hydraenidini Perkins) 10

9′. Hypomeral carina separated from notosternal suture by narrow band of hydrofuge pubescence that is continuous with pubescence of postcoxal pronotal projection (Fig. 61A); setae on margin of wet-hypomeron larger, pocket-forming (Fig. 62B:a); last abdominal sternum of female concealed beneath sixth, or only distal nonsetose margin exposed; southern Africa, Madagascar, and India (Madagastrini new tribe) 12

10. Antennal pocket open dorsolaterally (Fig. 55); abdomen with first and lateral thirds of second sterna hydrofuge pubescent, remainder with sparse, more robust setae; elytra posteriorly narrowed and transversely convex; aedeagus lacking parameres; aquatic species; Ecuador *Haptaenida* n. gen.

10′. Antennal pocket not open dorsolaterally; abdominal pubescence not as above; elytra not as above; aedeagus with parameres, although sometimes reduced 11

11. Pronotum subcordate, sides sinuate near posterior angles; elytra with serial rows of punctures in sulcate impressions, intervals costate or subcostate; aedeagus with left paramere originating near apex, right paramere absent or reduced to small spike near apex; hygropetric; South America . . . . *Parhydraenida* J. Balfour-Browne

11′. Pronotum with sides straight near posterior angles; elytra with serial rows of punctures not in sulcate impressions, intervals flat or slightly rounded; aedeagus with both parameres elongate, originating near base; aquatic; Chile . . . . *Hydraenida* Germain

12. Head with frons concave between protuberant and elevated eyes; hypomeral antennal pocket lacking band-like strip of reticulation at medial margin; antenna with combined lengths of first two articles slightly greater than remainder of antenna; hygropetric; eastern and southern Africa . . . . *Coelometopon* Janssens

12′. Head not as above; hypomeral antennal pocket with band-like strip of reticulation at medial margin (antennal cleaner?; Fig. 63B:c); antenna with combined lengths of first two articles much shorter than remainder of antenna 13

13. Pronotum deeply excavate at posterior angles (Fig. 61A); elytra with ten series of punctures; elytra with sutural interval, even-numbered interseries and lateral margin each costate and bearing unilinear row of granule-based setae (Fig. 61C); humicolous; southern India . . . . *Davidraena* Jäch

13′. Pronotum lacking excavations at posterior angles; elytra with four costae (on homologues of even-numbered intervals), some interrupted, costae separated one from the other by three or four rows of punctures, punctures sometimes not serial; hygropetric; Madagascar . . . . *Madagaster* n. gen.

Key to Tribes, Subtribes, and Genera of Ochthebiinae

1. Antenna with 11 articles; lacinia bearing many brush-like, slender setae; maxillary palpi arching, apex directed ventrad, second article arcuate; ocelli located near midline of frons; tentorium lacking wall-like anterior thickening; antennal pockets lacking specialized ESDS structures; fungicolous species; southern Chile (Ochtheosini new tribe) . . . *Ochtheosus* n. gen.

1′. Antenna comprised of nine or eight articles; lacinia bearing enlarged, stout apical teeth; maxillary palpi not distinctly arching ventrad; ocelli more widely separated, not located near midline of frons; tentorium with wall-like anterior thickening with a central "foramen"; antennal pockets with or without specialized ESDS structures (Ochthebiini Thomson) 2

2. Abdomen (both sexes) with seventh (last) sternum concealed beneath sixth, or just distal margin exposed, with micropores, but lacking setae; aedeagus lacking parameres, main-piece not markedly arcuate basally; last abdominal sternum of males without strut; antennal club not set at an angle to preclub (morphological sixth) article, latter not cupuliform, or only very slightly so; antennal pocket without specialized ESDS structures (Meropathina new subtribe) 6

2′. Abdomen (both sexes) with seventh (last) sternum exposed and bearing setae; aedeagus with parameres, main-piece basally arcuate; last abdominal sternum of males with strut; antennal club set at an angle to cupuliform preclub (morphological sixth) article, or articulating with latter such that an angle can be formed; antennal pocket with or without specialized ESDS structures 3

3. Prothorax without wet-hypomeron; hypomeral antennal pocket entirely microreticulate; postocular area without specialized ESDS structures; profemur without distal spine cluster 4

3′. Prothorax with wet-hypomeron delimited medially by hypomeral hyaline border; hypomeral antennal pocket not entirely microreticulate; postocular area with specialized ESDS structures; profemur with or without distal spine cluster 5

4. Prothorax without hypomeral hyaline border; head without transgenal sulcus; antenna with second article tapering distally, third article distally enlarged, shorter than second; eyes reduced; aquatic, intertidal; Japan and western U.S.A. (Neochthebiina new subtribe) . . . . *Neochthebius* Orchymont

4′. Prothorax with hypomeral hyaline border at lateral margin of hypomeron, horizontally oriented; head with transgenal sulcus; antenna with second article truncate distally, third article narrow throughout, longer than second; eyes not reduced; aquatic: Nepal (Protochthebiina new subtribe) . . . . *Protochthebius* n. gen.

5. ESDS with smooth postocular secretion delivery (psd-) shelf and psd-setae with brush-like tips; hypomeral hyaline border wide at anterior extreme; hypomeral antennal pocket (hap-) setae short relative to width of hypomeral hyaline border; aquatic; Palearctic and Nearctic (Enicocerina new subtribe) . . . . *Enicocerus* Stephens

5′. ESDS with secretion delivery area consisting of sulcus (either postocular or transgenal) or spiculate area; psd-setae of various forms; hypomeral antennal pocket (hap-) setae of variable length, usually much longer than anterior extreme of hypomeral hyaline border (Ochthebiina Thomson) 8

6. Hypomeral antennal pocket shallow, hydrofuge pubescent except narrow lateral marginal band (Fig. 41); postocular area lacking carina; antenna with second article ovoid, not cupuliform; metasternum reduced, entirely hydrofuge pubescent; dorsum with strong recumbent setae; terrestrial, coastal (porous rock, bird nests, grass tussocks, under stones); New Zealand, sub-Antarctic islands and islands at southern tip of South America . . . . *Meropathus* Enderlein

6′. Hypomeral antennal pocket deeper, hydrofuge pubescence restricted to about medial half (Fig. 42A:i, 44A:i); postocular carina or ridge distinct; antenna with second article large, distal end cupuliform (Fig. 43C:y); metasternum not reduced, with large median glabrous area; dorsal vestiture various 7

7. Wet-hypomeron anteriorly enclosing part of antennal pocket, margin bearing large, strong setae (two or four; Fig. 44:g, 45:g); hypomeral carina distinct, dividing wet- and bubble-hypomeron (Fig. 44C); venter of head lacking longitudinal ridges; prosternum lacking antennal cleaner; metasternum with large median, convex glabrous area; dorsal vestiture various; aquatic, splash zone, and hygropetric; eastern Australia and Tasmania .... *Tympanogaster* Janssens

7′. Hypomeron entirely concave anteriorly, lacking wet-hypomeron delimited by hypomeral carina (Fig. 42A:i); venter of head with three, longitudinal submental ridges (Fig. 43A:m); prosternum with two clusters of spines (antennal cleaner?; Fig. 43B:a); metasternum with midlongitudinal impression; dorsum with strong, recumbent setae; humicolous; southwestern Australia .... *Tympallopatrum* n. gen.

8. Head with transgenal secretion sulcus, cuticle raised on each side of sulcus to form transgenal ridge (Fig. 40:z); psd-setae elongate, with tapering tips; hh-border large anteriorly, contacting psd-setae (Fig. 40:o); hap-setae not extended beyond margin of hh-border; posterior border of pronotum arcuate, without distinct posterior angles; hh-border contiguous with ph-border, lh-border absent; profemur without distal spine cluster; meso- and metacoxae transversely well separated (in derived condition); aquatic, coastal rockpools; southern Australia, northern Tasmania .... *Hughleechia* Perkins

8′. Head without transgenal secretion sulcus; psd-setae various; prothorax with hh- and lh-borders in addition to ah- and ph-borders; profemur with distal spine cluster; pronotum with distinct posterior angles 9

9. Venter of head near posteroventral angle of eye with strongly microreticulate shelf that terminates in spiculate secretion area (Fig. 38:z, 39:z); plumose secretion delivery setae, each with multiply branched tips, adjacent to spiculate secretion area (Fig. 38:a, 39:a); hap-setae short, extending only slightly beyond margin of lh-border (Fig. 38A:g); aquatic; eastern Australia .... *Gymnanthelius* n. gen.

9′. Head at posteroventral angle of eye with psd-sulcus (e.g., Fig. 29:c); psd-setae of various forms, but not plumose 10

10. Psd-sulcus continuous with transgenal ridge (Fig. 37:z); psd-setae short, slightly widened from base to apex, flattened, and apically fringed (Fig. 37:a); hap-setae about twice as long as width of hh-border (Fig. 37:g); pronotum with two deep transverse grooves, one in front of and one behind middle, connected by median longitudinal groove; pronotal anterior angles lobate; vestiture of ventrites consisting of hydrofuge setae and stiff, erect spines; aedeagus with gonopore at apex of mainpiece, not on preapical distal piece; body size very small; aquatic; Old World .... *Aulacochthebius* Kuwert

10′. Head without transgenal ridge; psd-setae elongate, tapering to pointed apices, often flattened; hap-setae elongate, contacting psd-setae (e.g., Fig. 1A, 2A); pronotum not as above; body size usually larger 11

11. Aedeagus with gonopore at apex of bifurcate main-piece; pronotal anterior angles usually lobate; vestiture of ventrites consisting of hydrofuge setae and stiff, erect spines; aquatic; North and South America and Australia .... *Gymnochthebius* Orchymont

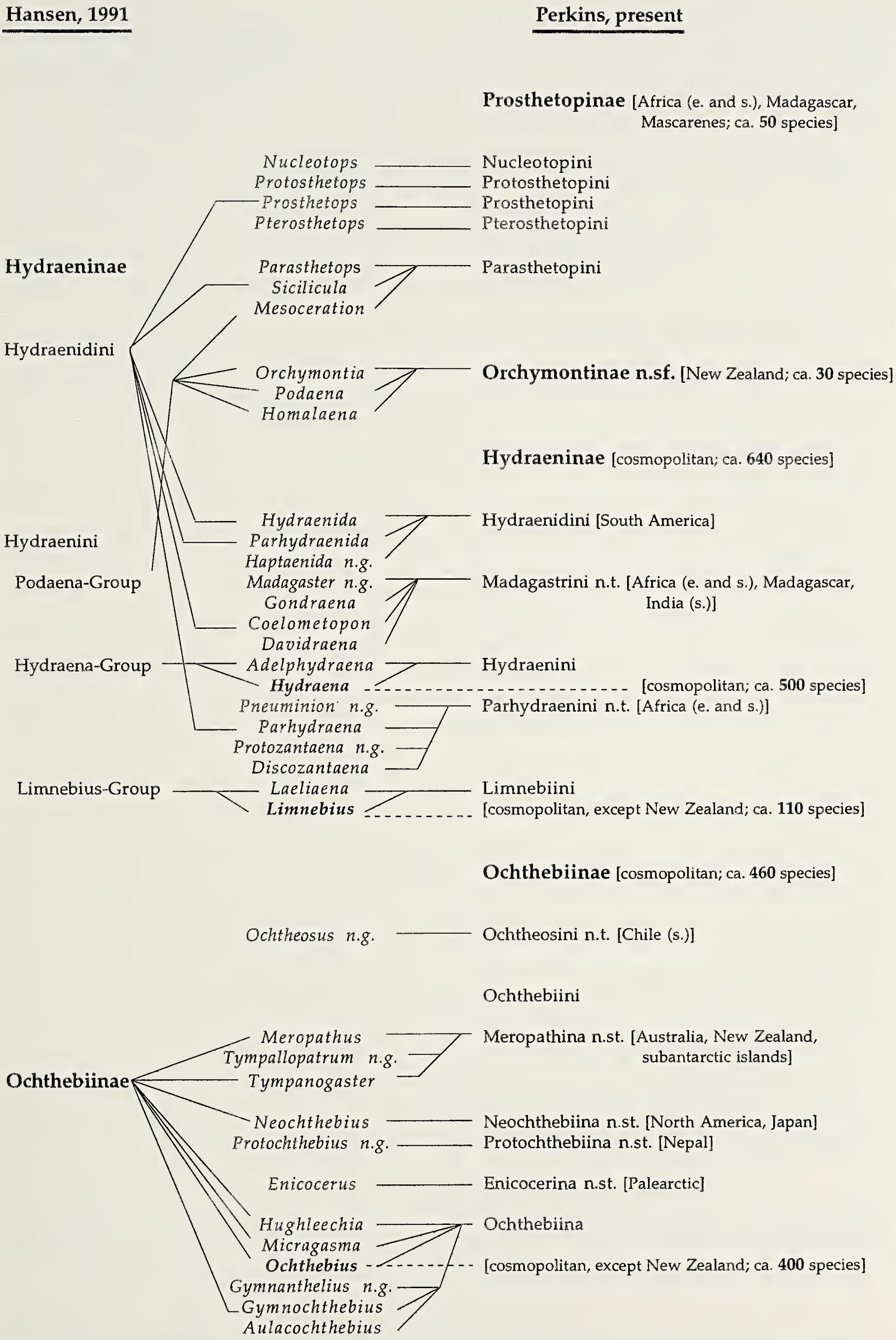
11′. Aedeagus with gonopore at apex of mobile distal piece that originates preapically on mainpiece; pronotal anterior angles not lobate; vestiture of ventrites hydrofuge setae without spines; aquatic; nearly cosmopolitan .... *Ochthebius* Leach

CONCLUSIONS

The antennal pocket of hydraenids, formed by adjacent areas of the head and prothorax, provides a rich array of new characters that are pivotal to our understanding of morphological change and phylogenetic relationships within the family. The complexity and integration of the parts of the antennal pocket are seen in their greatest expression in the specialized ESDS of *Ochthebius, Hydraena,*

→

Fig. 71.—Relationships and classification of the Hydraenidae as given by Hansen (1991) and as proposed herein. Putative synapomorphic and plesiomorphic characters of groups are discussed in the text and summarized in the key to taxa. Numbers of described species are approximate. The genera *Ochthebius, Hydraena,* and *Limnebius* comprise about 85% of described species.


Hansen, 1991
Perkins, present
Prosthetopinae [Africa (e. and s.), Madagascar, Mascarenes; ca. 50 species]
Nucleotops
Nucleotopini
Protosthetops
Protosthetopini
Prosthetops
Prosthetopini
Pterosthetops
Pterosthetopini
Hydraeninae
Parasthetops
Parasthetopini
Sicilicula
Mesoceration
Hydraenidini
Orchymontia
Orchymontinae n.sf. [New Zealand; ca. 30 species]
Podaena
Homalaena
Hydraeninae [cosmopolitan; ca. 640 species]
Hydraenida
Hydraenidini [South America]
Hydraenini
Parhydraenida
Haptaenida n.g.
Podaena-Group
Madagaster n.g.
Madagastrini n.t. [Africa (e. and s.), Madagascar, India (s.)]
Gondraena
Coelometopon
Davidraena
Hydraena-Group
Adelphydraena
Hydraenini
Hydraena
[cosmopolitan; ca. 500 species]
Pneuminion n.g.
Parhydraenini n.t. [Africa (e. and s.)]
Parhydraena
Protozantaena n.g.
Discozantaena
Limnebius-Group
Laeliaena
Limnebiini
Limnebius
[cosmopolitan, except New Zealand; ca. 110 species]
Ochthebiinae [cosmopolitan; ca. 460 species]
Ochtheosus n.g.
Ochtheosini n.t. [Chile (s.)]
Ochthebiini
Meropathus
Meropathina n.st. [Australia, New Zealand, subantarctic islands]
Tympallopatrum n.g.
Ochthebiinae
Tympanogaster
Neochthebius
Neochthebiina n.st. [North America, Japan]
Protochthebius n.g.
Protochthebiina n.st. [Nepal]
Enicocerus
Enicocerina n.st. [Palearctic]
Hughleechia
Ochthebiina
Micragasma
Ochthebius
[cosmopolitan, except New Zealand; ca. 400 species]
Gymnanthelius n.g.
Gymnochthebius
Aulacochthebius

and *Limnebius,* genera that have evolved secretion-grooming behavior. The relative success of these three genera, by far the most speciose (comprising nearly 85% of described species) and the most widely distributed in the family (Fig. 71), is surely related to their ability to maintain effective respiratory bubbles.

Knowledge of the ESDS provides new perspectives on the utilization of aquatic microhabitats by hydraenids. Streams and ponds are nearly worldwide, forming networks of microhabitats across a widely variable matrix of climatic, edaphic, and biotic conditions. Among hydraenids, the genera with specialized ESDS have been overwhelmingly successful in these stream and pond microhabitats. The proposition that the ESDS is pivotal to opening these widespread microhabitats to hydraenids is strengthened by the three-fold independent evolution of specialized ESDS.

However, although the genera *Ochthebius, Hydraena,* and *Limnebius* are common in sandy–gravelly stream margin and pond margin microhabitats, only very occasionally is a specimen of these genera found in hygropetric microhabitats, such as rock face seeps or margins of waterfalls, and members of the three genera are never benthic. This suggests that the specialized ESDS is not readily modified, via either amplification or reduction, to allow utilization of the hygropetric and benthic microhabitats. Certainly many aspects of hydraenid biology are involved in this microhabitat restriction, but one obvious possibility is that secretion-grooming behavior, which occurs out of the water, is an effective deterrent to life on vertical, wet rock faces or stream bottoms.

Contrastingly, benthic microhabitats are utilized by members of the Prosthetopinae and Orchymontinae, hydraenids that have virtually no antennal pocket. Instead of a bubble, benthic species have a thin layer of air held by plastron vestiture, eliminating the need to return to the surface for air. Reflecting the loss of the respiratory bubble-replenishing function, the antennae of these forms are in various stages of reduction and fusion, occurring independently in several lineages (Perkins and Balfour-Browne, 1994). Significantly, the antennae of some members of both the Prosthetopinae and Orchymontinae retain the condition of 11 articles, the plesiomorphic number for the family. These plesiomorphic antennae are obviously not derived from the antennae of forms with specialized ESDS, which have the preclub articles reduced in number and shaped to conform to the antennal pocket. Accepting the commonly held premise that loss of antennal articles by fusion and reduction is unidirectional, then it necessarily follows that the Prosthetopinae and Orchymontinae are not derived from any clades with specialized ESDS, all of which have loss of preclub antennal articles. The absence of an antennal pocket therefore does not represent secondary reduction from the well-formed and complex antennal pocket of ESDS lineages.

Similar antennal evidence is available for humicolous and hygropetric forms. The only Ochthebiinae retaining the ancestral, 11-articled antenna is *Ochtheosus,* a fungicolous species with primitive mouthparts and primitive internal head structure. In the Hydraeninae, seven of the 12 genera have 11-articled antennae; three of these genera are definitely hygropetric (*Parhydraenida, Coelometopon,* and *Madagaster*), one possibly hygropetric (*Hydraenida*), and one is humicolous (*Davidraena*). Genera with 11-articled antennae are not derived from lineages with the reduced antenna characteristic of genera with specialized ESDS.

The secondary loss of structures is always a possibility that should be addressed. For example, it is possible that the lack of ESDS structures in *Neochthebius* (Fig. 46, 47) is the result of secondary loss due to the unusual microhabitat (cracks in intertidal rocks). However, such a reversal would require the loss without a trace of a complete character system, not just the reduction of one or two components. Some evidence, for example the retention of the periocular exocrine pores of *Meropathus,* which has reduced eyes (Fig. 41B:e), indicates that at least some exocrine-related structures are not readily lost, despite reduction of surrounding body areas. Postulating secondary losses on the absence of clear supporting evidence would be premature; such losses (if any have occurred) must be uncovered by new findings.

There are strong correlations in the body forms of hydraenids and the various specialized ESDS. I have wondered why members of *Hydraena* are so "loosely jointed" compared with other hydraenids. The ESDS explanation is that the extensive intersegmental membranes make it possible for the tibiae to effectively clean the hypomeron during secretion-grooming, by allowing extending and twisting of the prothorax. *Limnebius* has an unusual shape, being the only hydraenid having the prothorax posteriorly wide and concave, with the distal end of the middle femur fitting into the concavity; this form correlates exactly with the location of the ESDS glandular fovea and secretion-grooming behavior. The characteristic hyaline borders of *Ochthebius* is another example of the relationship of specialized body form and the ESDS.

This paper is only the beginning of our understanding of the ESDS and the antennal pocket, and the relationships of these features to the natural history and phylogeny of the family. Observations of secretion-grooming behavior and bubble formation are needed for more species of *Ochthebius, Hydraena,* and *Limnebius.* Grooming behavior of the remainder of the family is entirely unstudied, and certainly more new genera remain to be discovered and described. A more comprehensive view of the phylogeny of hydraenids will require these studies, in addition to a detailed morphological study of the larval forms in the family.

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APPENDIX 1

Taxa Studied in Transparency Mounts, and New Combinations(!)

Orchymontinae

Homalaena dispersa Ordish (New Zealand), *Orchymontia ciliata* Ordish (New Zealand), *O. spinipennis* Broun (New Zealand), *Podaena dentipalpis* Ordish (New Zealand).

Prosthetopinae

Mesoceration abstrictum Perkins and B.-Browne (South Africa), *M. apicalum* Perkins and B.-Browne (South Africa), *M. brevigranum* Perkins and B.-Browne (South Africa), *M. dissonum* Perkins and B.-Browne (South Africa), *M. distinctum* Perkins and B.-Browne (South Africa), *M. endroedyi* Perkins and B.-Browne (South Africa), *M. fusciceps* Perkins and B.-Browne (South Africa), *M. jucundum* Perkins and B.-Browne (South Africa), *M. languidum* Perkins and B.-Browne (South Africa), *M. rivulare* Perkins and B.-Browne (South Africa), *M. rubidum* Perkins and B.-Browne (South Africa), *M. rufescens* Perkins and B.-Browne (South Africa), *M. splendorum* Perkins and B.-Browne (South Africa), *M. sulcatulum* Perkins and B.-Browne (South Africa), *M. transvaalense* Janssens (South Africa), *M. truncatum* Perkins and B.-Browne (South Africa).

Nucleotops nimbaceps Perkins and B.-Browne (South Africa), *Parasthetops aeneus* Perkins and B.-Browne (South Africa), *P. camurus* Perkins and B.-Browne (South Africa), *P. curidius* Perkins and B.-Browne (South Africa), *P. nigritus* Perkins and B.-Browne (South Africa), *P. reflexus* Perkins and B.-Browne (South Africa), *P. rufulus* Perkins and B.-Browne (South Africa), *P. spinipes* Perkins and B.-Browne (South Africa), *Prosthetops grandiceps* Perkins and B.-Browne (South Africa), *P. megacephalus* (Boheman) (South Africa), *P. nitens* (Péringuey) (South Africa), *P. setosus* Perkins and B.-Browne (South Africa), *Protosthetops kenyensis* (Orchymont) (Kenya), *Pterosthetops equestrius* Perkins and B.-Browne (South Africa), *P. harrisoni* Perkins and B.-Browne (South Africa), *P. impressus* Perkins and B.-Browne (South Africa), *Sicilicula borbonica* J. Balfour-Browne (Reunion).

Hydraeninae

Adelphydraena orchymonti Perkins (Venezuela), *Coelometopon madidum* Janssens (Tanzania), *Coelometopon* (two n. spp., South Africa), *Davidraena bacata* n. gen., n. sp. (India), *Discozantaena genuvela* Perkins and B.-Browne (South Africa), *Hydraena* (*Haenydra*) *gracilis* Germar (France), *Hydraena* (*Hadrenya*) *minutissima* Stephens (!) (Germany), *H.* (*Hadrenya*) *pygmaea* Waterhouse (!) (Germany), *H.* (*Hadrenya*) *sharpi* Rey (!) (Spain), *Hydraena* (*Phothydraena*) *testacea* Curtis (United Kingdom, Spain).

Hydraena (sensu stricto) *accurata* Orchymont (South Africa), *H.* (sensu stricto) *americana* Jäch (U.S.A.), *H.* (sensu stricto) *angulosa* Mulsant (France), *H.* (sensu stricto) *anisonycha* Perkins (Colombia), *H.* (sensu stricto) *brevis* (Sharp) (!) (Mexico), *H.* (sensu stricto) *circulata* Perkins (U.S.A.), *H.* (sensu stricto) *cuspidicollis* Perkins (Mexico), *H.* (sensu stricto) *exarata* Kiesenwetter (Spain), *H.* (sensu stricto) *finita* Orchymont (Greece), *H.* (sensu stricto) *occidentalis* Perkins (U.S.A.), *H.* (sensu stricto) *pulchella* Germar (Slovenia), *H.* (sensu stricto) *riparia* Kugelann (France), *H.* (sensu stricto) *stussineri* Kuwert (Spain), *H.* (sensu stricto) (15 n. spp., Australia, Papua New Guinea, South Africa).

Hydraenida ocellata Germain (Chile), *H. robusta* Perkins (Chile), *Laeliaena* (n. sp., Nepal), *Limnebius hispanicus* Orchymont (Spain), *L. piceus* (Horn) (U.S.A.), *L. sinuatus* Sharp (Guatemala), *L. truncatellus* Thomson (Portugal), *Limnebius* (five n. spp., Australia, South Africa).

Madagaster steineri n. gen., n. sp. (Madagascar), *Parhydraena brevipalpis* (Régimbart) (Ethiopia), *P. jeanneli* (Orchymont) (!) (Kenya), *P. seriata* J. B.-Browne (South Africa), *Parhydraena* (five n. spp., South Africa), *Parhydraenida bubrunipes* Perkins (Brazil), *Pneuminion velamen* n. gen., n. sp. (South Africa), *Protozantaena labrata* n. gen., n. sp. (South Africa).

Ochthebiinae

Enicocerus benefossus (LeConte) (!) (U.S.A.), *E. exsculptus* (Germar) (!) (France), *Gymnanthelius clypeatus* (Deane) (!) (Australia), *G. hieroglyphicus* (Deane) (!) (Australia), *Gymnochthebius brisbanensis* (Blackburn) (!) (Australia), *G. fossatus* (LeConte) (Mexico), *G. germaini* (Zaitzev) (Chile), *G. laevipennis* (LeConte) (U.S.A.), *G. lividus* (Deane) (!) (Australia), *G. maureenae* Perkins (U.S.A.), *G. notalis* (Deane) (!) (Australia), *G. octonarius* Perkins (Argentina), *G. oppositus* Perkins (U.S.A.), *G. perlabidus* Perkins (Costa Rica), *G. plesiotypus* Perkins (Argentina), *Gymnochthebius* (four n. spp., Australia, New Guinea).

Hughleechia giulianii Perkins (Australia), *Meropathus campbellensis* Brookes (Campbell Island), *M. vectis* Perkins (Argentina), *Micragasma paradoxum* J. Sahlberg (Greece), *Neochthebius vandykei* (Knisch) (U.S.A.).

Ochthebius (*Asiobates*) *andronius* Orchymont (South Africa), *O.* (*A.*) *angularidus* Perkins (U.S.A.), *O.* (*A.*) *apache* Perkins (U.S.A.), *O.* (*A.*) *bicolon* Germar (United Kingdom), *O.* (*A.*) *brevipennis* Perkins (U.S.A.), *O.* (*A.*) *cribricollis* LeConte (U.S.A.), *O.* (*A.*) *discretus* LeConte (U.S.A.), *O.* (*A.*) *leechi* Wood and Perkins (U.S.A.), *O.* (*A.*) *martini* Fall (U.S.A.), *O.* (*A.*) *puncticollis* LeConte (U.S.A.), *O.* (*A.*) *similis* Sharp (U.S.A.).

Ochthebius (sensu stricto) *adriaticus* Reitter (!) (Greece), *O.* (sensu stricto) *arenicolus* Perkins (U.S.A.), *O.* (sensu stricto) *aztecus* Sharp (Mexico), *O.* (sensu stricto) *batesoni* Blair (Ecuador), *O.* (sensu stricto) *borealis* Perkins (U.S.A.), *O.* (sensu stricto) *capicola* (Péringuey) (South Africa), *O.* (sensu stricto) *caucasicus* Kuwert (India), *O.* (sensu stricto) *celatus* Jäch (!) (Malta), *O.* (sensu stricto) *difficilis* Muls. (Spain), *O.* (sensu stricto) *eburneus* J. Sahlberg (!) (Tunisia), *O.* (sensu stricto) *extremus* (Péringuey) (South Africa), *O.* (sensu stricto) *glaber* Montes and Soler (Spain), *O.* (sensu stricto) *interruptus* LeConte (U.S.A.), *O.* (sensu stricto) *lejolisi* Mulsant and Rey (!) (France), *O.* (sensu stricto) *lineatus* LeConte (U.S.A.), *O.* (sensu stricto) *marinus* (Paykull) (U.S.A.), *O.* (sensu stricto) *namibiensis* Perkins and B.-Browne (Namibia), *O.* (sensu stricto) *notabilis* Rosenhauer (Spain), *O.* (sensu stricto) *obscurus* Sharp (U.S.A.), *O.* (sensu stricto) *pagotrichus* Perkins and B.-Browne (Namibia), *O.* (sensu stricto) *pedalis* J. B.-Browne (South Africa), *O.* (sensu stricto) *pedicularius* Kuw. (Spain), *O.* (sensu stricto) *punctatus* Stephens (Spain), *O.* (sensu stricto) *quadricollis* Mulsant (!) (Madeira, Sardinia), *O.* (sensu stricto) *quadrifoveolatus* Wol. (Spain), *O.* (sensu stricto) *recticulus* Perkins (U.S.A.), *O.* (sensu stricto) *rectus* LeConte (U.S.A.), *O.* (sensu stricto) *rubripes* Boheman (!) (Namibia), *O.* (sensu stricto) *salinarius* J. B.-Browne (South Africa), *O.* (sensu stricto) *salinator* Peyerimhoff (Egypt), *O.* (sensu stricto) *serratus* Rosenhauer (!) (Morocco), *O.* (sensu stricto) *spatulus* J. B.-Browne (South Africa), *O.* (sensu stricto) *spinasus* Perkins and B.-Browne (South Africa), *O.* (sensu stricto) *subinteger* Mulsant and Rey (!) (Morocco), *O.* (sensu stricto) *uniformis* Perkins (U.S.A.), *O.* (sensu stricto) *zugmayeri* Knisch (Iran).

Ochtheosus fungicolus n. gen., n. sp. (Chile), *Protochthebius jagthanae* (Champion) (!) (Nepal), *P. satôi,* n. gen., n. sp. (Nepal), *Tympallopatrum longitudum* n. gen., n. sp. (Australia), *Tympanogaster* *cornutus* (Janssens) (!) (Australia), *T. deanei* Perkins (Australia), *T. macrognathus* (Lea) (!) (Tasmania), *Tympanogaster* (three n. spp., Australia).

APPENDIX 2

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